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# The Functional Morphology of the Egg-eating Adaptations in the Snake Genus *Dasypeltis*

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(Plates I-IV; Text-figures 1-15)

### INTRODUCTION

THE snakes of the genus *Dasypeltis,* and perhaps those of the much less well known genus *Elachistodon,* present one of the most striking series of adaptations to a specialized feeding habit exhibited by any of the Serpentes. While *Coluber scaber* and some of its peculiarities were described by Linnaeus as far back as 1754 and his diagnosis of that date contained the phrase "Dentes nulli" (1754, p. 36), it was not until eighty years later that this singular feature of the animal was investigated further. Since that time a variety of studies and observations, dealing with both the morphology and habit of the form, have been published, but no complete analysis of the function of the various modifications has ever been presented. This becomes particularly evident when one examines and compares the discussions of this snake in various recent natural histories and semi-popular treatises.

The present studies were prompted by the discovery of certain adaptations to egg-eating in a group of East Asiatic snakes (Gans & Oshima, 1952). Before the taxonomic position of these species, generally considered to belong to the colubrid genus *Elaphe,* could be established, it seemed desirable to determine the exact extent of the modifications present in the case of *Dasypeltis.*

This study, therefore, forms an attempt at an evaluation of the modifications in *Dasypeltis,* and a provisional analysis of their function, as well as a summation of the data to be utilized in a later re-examination of the taxonomic position of this genus. It has been based upon an examination of the literature as well as on an extensive review of both alcoholic and skeletal material in various museums. It was initially intended to include the results of studies, presently in progress, on living specimens; however, for various reasons these results will have to be reported on at a future date.

No attempt has been made here to retrace previous studies completely wherever the material checked appeared to be in reasonable agreement with the published data. Since it was found that some morphological variation seemed to exist between the different subspecies presently recognized, and since the status of these was very indefinite over large regions of Africa, a detailed analysis of the systematics involved has seemed imperative. Such an investigation is presently under way jointly by Mr. Arthur Loveridge of the Museum of Comparative Zoology and the writer, and we intend to publish the results at a later date.

### ACKNOWLEDGMENTS

This study was based on material from a number of institutions and for these loans as well as for permission to perform anatomical observations and to skeletonize certain specimens I am indebted to Mr. C. M. Bogert and Mrs. Bessie M. Hecht of the American Museum of Natural History; Messrs. M. G. Netting and Neil D. Richmond of the Carnegie Museum; Messrs. C. H. Pope and D. D. Davis of the Chicago Natural History Museum; Mr. A. Loveridge of the Museum of Comparative Zoology at Harvard College; Dr. N. Hartweg and Mr. James A. Peters of the University of Michigan Museum of Zoology; Mr. C. F. Kauffeld of the Staten Island Zoological Society; and Dr. Doris M. Cochran of the United States National Museum.

I am most grateful to Mr. Charles M. Bogert for the use of departmental laboratory and library facilities during the course of this study, for his review of the manuscript and for his many helpful suggestions; and to Mr. Arthur Loveridge for use of the collection and laboratory, as well as for his help in obtaining live material. To Dr. Ernest E. Williams I am extremely grateful for his many helpful suggestions and general aid during the course of the work. Dr. Paulo E. Vanzolini put me into his debt by his careful review of the section on morphology and by supplying the information regarding his method of skeletonization.

I should also like to express my appreciation to Mr. S. B. McDowell who prepared the drawings; Mr. Sam Dunton, Staff Photographer of the New York Zoological Park, for information relating to the excellent series of photographs that he made of the feeding process; the New York Zoological Society for the use of photographs; Dr. K. F. Koopman who prepared the preliminary bibliography; Miss Hazel Gay and staff of the American Museum library for help with bibliographic work; Mrs. Anita Gans who typed the manuscript; and to my brother, Leo Gans, without whose help it probably would have proved impossible to complete this project.

During the course of the work I repeatedly had the opportunity to discuss problems relating thereto with Dr. Ernest E. Williams of the Museum of Comparative Zoology, Dr. James A. Oliver of the New York Zoological Society and Dr. Paulo E. Vanzolini of the Departamento de Zoologia of Sao Paulo, Brazil, all of whom also read the manuscript and offered many helpful comments. Phases of the problem were also discussed with Dr. A. d'A. Bellairs, Mr. Max K. Hecht, Mrs. Bessie M. Hecht, Dr. Karl F. Koopman, Mr. S. B. McDowell and Mr. Neil D. Richmond. These discussions brought forth some very stimulating ideas. None of these friends is, however, to be blamed for the shortcomings of this study.

## MATERIALS AND METHODS

A large number (175+) of specimens from various institutions was examined for external and internal characters and a variety of dissections and examinations of skeletal material were made. The numbers of those specimens on which more detailed examinations were performed are listed below, following the list of abbreviations and the sources of specimens.

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| AMNH | American Museum of Natural History, New York |
| CFK | Carl F. Kauffeld, personal collection, New York |
| CM | Carnegie Museum, Pittsburg, Pa. |
| CNHM | Chicago Natural History Museum, Chicago, Ill. |
| MCZ | Museum of Comparative Zoology, Cambridge, Mass. |
| UMMZ | Museum of Vertebrate Zoology, University of Michigan, Ann Arbor, Michigan |
| USNM | United States National Museum, Washington, D. C. |

The drawings in the paper are occasionally composites and the characters depicted in any one of them were compared with those of a large number of specimens to insure their general accuracy. This was done in an attempt to eliminate individual variations of a trivial nature (such as aberrations in chin shield shape). Hence, the individual drawings have not been referred to specific specimens.

In dealing with the morphology of the snake, three general investigatory techniques were employed, namely: external examination, macrodissection and skeletonization. The first involved examination of oral and integumentary characters under a binocular dissecting microscope and was performed for all specimens. The status of the esophageal penetration, muscle attachments and the kinetics of the skull was checked by macrodissection, for which purpose needles and blunt probes were utilized. All such dissections were performed under the binocular microscope; however, no histological examinations were made.

Most of the skeletal material was prepared by me after detailed dissection, although skeletons from various collections were used for comparison purposes. For the particular method of skeletonization I am very much indebted to Dr. P.E.Vanzolini who developed it. This technique consists of repeatedly immersing the partially-cleaned specimen in full strength commercial bleach (Clorox, etc.). Between immersions the specimen is dried under an infra-red lamp after first being washed. This assures that full strength bleach is always acting on all the soft tissues, even those partially protected by bone, and consequently reduces the total time the bone has to be exposed to the action of the corrosive fluid. For small specimens such as juvenile *Dasypeltis* the process has to be carefully checked and controlled and care must be taken that the bones are thoroughly washed prior to storage. The method is unexcelled for speed and little care is required in preparing skeletal material of larger species. An experienced technician is easily able to prepare three to five large skulls in an afternoon.

In view of the fact that the subspecific and possibly also the specific position of the various forms is in doubt, reference has here been made only to the museum numbers of the individual specimens. It is felt that localities and other data more properly belong with that portion of this study dealing with the taxonomy of the genus, which is to be published later.

Skeletonizations or examinations of existing portions of the vertebral column or of the skull were performed for the following specimens: AMNH Nos. 2403 and 57861; CFK Nos. 1 and 2; CM No. 9240; CNHM Nos. 17677 and 19455; MCZ Nos. 13202, 30208, 48381 and 48389; UMMZ No. S-130; and USNM No. 62901.

One cleared and stained specimen (AMNH No. 46474, prepared by Mrs. Bessie M. Hecht) was utilized to determine the position of the hyoid.

Besides the general check of the entire series of specimens, more thorough examinations of oral as well as internal aspects were made on the following specimens: AMNH Nos. 7685, 12184, 12185, 12186, 12187, 12188, 12201, 18218, 20345, 31638, 50596, 50597, 50600, 50601, 50602, 50603, 50791 and 57861; CNHM Nos. 12823, 12824, 16755 and 24175; MCZ Nos. 6033 and 24745; UMMZ Nos. 88531, 96274 and 96756; and USNM Nos. 40990 and 49376.

## Historical

*Systematic.*—As mentioned in the introduction, Linnaeus first described *Coluber scaber* in 1754 (Vol. 1, p. 36, pl. 10, fig. 1). The name technically dates from the tenth edition of the "Systema Naturae" published in 1758 (p. 223). Andrew Smith (1829, p. 443) erected the family Anodontidae and the genus *Anodon* for this single species, still believing it to be edentulous. Since the latter name was preoccupied by *Anodon* Oken (1815, p. 236), used for a mollusk, the name *Dasypeltis* Wagler (1830, p. 178) applies. Recently serious doubt has been cast on the availability of certain mammal names of Oken (Hershkovitz, 1949, p. 289) on the grounds that he was not a strict binominalist. However, since the name *Dasypeltis* appears to be almost universally recognized (and has been so used since 1830), I shall retain it here.[1]

Because of the extreme degree of infra-specific color variation and the fact that this has generally not proved to be correlated with any scale characters (Bogert, 1940, p. 85), the status of the various named forms is very confusing. The last major review of the genus (Loveridge, 1942, pp. 282-286)—based, however, on the forms of a limited area—resulted in the revival of several ecological subspecies of *D. scaber* (*scaber*, *fasciatus*, *medici*, *palmarum* and *inornatus*). As already stated, taxonomic considerations will be deferred until a later paper; therefore, Loveridge's nomenclature will be used in the present report.

*General.*—In the section that follows it is intended to give short summaries of published discussions of the morphology and habits of *Dasypeltis* that contribute to the present problem. A further number of books and papers referring to these topics, but insufficiently significant to be summarized, have been listed and annotated in the bibliography.

Although Linnaeus' original description indicated knowledge of the dentitional reduction, the attention of early herpetologists seems rather to have been caught by the presence of the rows of serrated lateral scales, utilized by the specimens to produce a rasping sound (Rose, 1950, p. 260). This is further reflected in the name "La Rude," "the rough snake" (Lacépède, 1789, p. 198). The initial discovery that there were other things of interest about this serpent was reported in 1834 in a paper read by Jourdan before the Académie des Sciences, and later abstracted in L'Institut (1834, p. 214)[2]. He found that, contrary to Linnaeus and Smith, seven teeth were present on each palatine and five on each maxilla, but more surprising to the naturalists of the time was his report that the anterior thirty (counted after the atlas axis complex) vertebral hypapophyses were modified structurally, covered with enamel ("revêtues d'une sorte d'émail") and pierced the esophagus. He also described the central musculature and aspects of the alimentary canal, and mentioned that the above modifications were utilized as an adaptation for egg-eating.

Saint-Hilaire (1834, p. 222) gave an interpretation of Jourdan's findings, in which he mentioned that the species ate eggs and suggested that since the teeth of the mouth were too small to break these, the "armor points like diamonds" in the esophagus had been provided by nature to compensate for this. Froriep (1834, pp. 104-105) presented a German abstract of

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[1] A petition has been addressed to the International Commission for Zoological Nomenclature asking that the name *Anodon* Smith, 1829, be set aside and that the name *Dasypeltis* Wagler, 1830, be placed on the list of *Nomina conservanda.*

[2] Numerous references appear in the literature to a paper by Jourdan in the Journal le Temps, of 13 June, 1833 or 1834. While extracts from and comments on Jourdan's work (see below) document the fact of its existence, I have been unable personally to verify the existence of this presumably complete version.

Jourdan's remarks, which he stated were made on June 30th, 1834.

That the status of publication of Jourdan's original study was already confused in 1844 is underlined by the fact that Duméril & Bibron (1844, p. 160) printed an abstract of his paper, which was more detailed than the account printed in the journal L'Institut, and stated that the abstracted paper had been published in the June 13th, 183? (sic) issue of the Journal le Temps.

Schlegel (1837, pp. 328-330) referred to *Tropidonotus scaber* in detail and specifically mentioned the fact that the lachrymal gland was larger here than in other species, extending from the eye to the angle of the jaw.

Owen in his "Odontography " (1840-1845, pp. 220-221) discussed the habit and adaptation of the form *(Deirodon),* stating that the egg was opened by the "spinous processes of the seven or eight posterior cervical vertebrae . . . capped with a layer of hard cement," which "saw" the shell open. He mentioned that these were present even in very young specimens and that the shell was swallowed. These identical remarks were later copied into his "Anatomy of the Vertebrates" (1866, p. 395).

Andrew Smith in his monumental "Illustrations of the Zoology of South Africa" (1849, plate 73 and text, p. 20, App.) both figured and described the modified vertebrae and the egg-eating process and also stated that the shell was ejected.

Duméril & Bibron described (1854, p. 487) and illustrated (1854, pl. 81, fig. 3) the skull and skeleton of the form. They mentioned the presence of teeth in the lower jaw and the fact that mainly the last seven hypapophyses penetrate the esophagus to act directly upon the egg. De Rochebrune (1881, p. 207) stated only that since others had covered the topic he would dispense with it.

Peters (1882, p. 119) mentioned teeth found on dentary, maxillary, palatine and pterygoid bones. He stated that several hypapophyses, their tips covered with enamel ("Schmelz"), penetrated the esophagus and that these were directed anteriorly to simplify regurgitation of the shell. Mocquard (1887, p. 81-83) commented on the fact that the first twelve hypapophyses were compressed in form and completely hidden by muscle tissue. He found these to be followed by six to seven vertebrae with rounded oval tubercles in turn followed by the seven others, whose hypapophyses were pointed and penetrated the gullet. He stated that, as already admitted by Duméril & Bibron (1854, p. 489), the twelve anteriormost were completely incapable of "sawing" through the egg's shell.

Hoffman (1890, pp. 1421) misquoted both Jourdan and Owen and went on to state that the dentitional reduction was advantageous in preventing fracture of the egg in the snake's mouth.

Tegetmeier in The Field (1892, p. 204) discussed *Dasypeltis,* presenting a drawing giving his impression of what it would look like with an egg in its throat, and also described the appearance of the ejected shell. Boulenger figured the skull in the "Catalogue of Snakes" (1894, p. 354) and in his diagnosis mentioned the presence of enamel on the hypapophyses and the absence of pterygoid teeth, and of a mental groove.

In 1896 Edith M. Durham (p. 715) gave what was probably the first description of the process of egg ingestion based upon actual observation. Her report, which is covered in more detail in the section on habits, mentioned that the specimen straightened its bent vertebral column, thus driving the spinal teeth into the egg. She timed the entire process from ingestion to regurgitation of the shell (for a canary's egg) at 1¾ hours and her simple line drawings and accurate description permit definite reconstruction of the process.

The first detailed morphological study of the anatomy of *Dasypeltis* was made by Kathariner (1898, p. 501) and the majority of his morphological findings have never been questioned, but almost universally ignored. His most important discovery lay in the demonstration that not enamel, but rather very dense bone, was present in the hypapophysial tips. He also stated that the oval knobbed tips of the mid-hypapophysial vertebrae were ridged (which is none too clearly apparent from his own figures) and believed that the egg was crushed by them. The rearmost spines were relegated to the function of facilitating the regurgitation of the shell. One of his three specimens was a juvenile, whose teeth were described as larger proportionally than those of the adults. He reasoned that this allowed the juvenile to ingest motile food until it achieved the size necessary to start eating eggs.

Anderson (1898, p. 278) figured a specimen with an egg in its mouth and quoted Andrew Smith on habits. He stated the time from ingestion to regurgitation as 15 minutes. Vaillant in a paper in the Comptes Rendues (1898, p. 1229), an expanded and illustrated version of which appeared in the semi-popular La Nature (1899, p. 97), speculated on the method used for holding the egg, and continued: "Deux replis membraneux que l'on peut observer sur notre individu aux parties latérales de la bouche, parleraient assez en faveur de cette manière de voir et pourraient bien servir à cet usage; chacun d'eux alternativement se fixerait comme ventouse, donnait ainsi un point d'appui pour permettre à l'autre de se pousser en avant." His figure of a mounted specimen with an egg in its mouth is interesting in that it correctly indicates the very peculiar position of certain chin scales during the swallowing process. He also stated that the shell was pierced, though in referring to the posterior hypapophysial vertebrae he used the misleading expression "un véritable scie (saw)."

Howes (1901, p. 320) attempted to reconstruct the crushing process, based upon a study of the fracture lines of two egg-shells obtained from the London Zoo. Gadow (1901, p. 622), while referring to Durham's paper (1896, p. 715) for a description of the habits, believed the function of the hypapophyses to lie in the filing through or breaking of the egg. Ferreira (1903, p. 10) presented a detailed discussion of the form, but mainly used Vaillant's paper for data.

F. W. FitzSimons in his book on the snakes of South Africa (1912, p. 102) devoted a large and rather amazing section to the African egg-eater. He appears to have believed that all the anterior as well as the intermediate hypapophysial vertebrae are functional as well as capped with enamel. The snake, when initially opening the egg, was described as raising its head above the ground, simultaneously working its backbone backwards and forwards and thus sawing through the shell. The function of the six or seven more strongly developed intermediate hypapophyses was to saw through the shells that the small ones could not manage. The only function of the posterior hypapophyses, correctly stated not to be covered with enamel, lay in keeping pieces of shell from slipping into the stomach. Besides detailed notes on methods of egg-swallowing and other habits, the book also presents two sets of photographs, both purporting to show the actual egg ingestion sequence. One of these (figs. 49-50) contains the statement in its caption that it is "the only one [pictorial sequence] of its kind in the world." One of these sets was later reproduced by Witte (1924, p. 40), who also copied FitzSimon's description of the ingestion method.

Ditmars (1912, p. 204) mentioned vertebrae with knife-like points, and stated that the few posteriorly situated teeth provided the power for the jaw bones alternately to grip and engulf the food, assisted by peristaltic movements of the muscles of the neck. In a later work (1922, p. 276) he restated what he had said in 1912, and also mentioned the fact that some specimens swallow the shell; in fact, "if the feast consists of the soft leathery shelled eggs of some other species of snake the integument of the eggs is invariably swallowed."

E. G. Boulenger (1914, p. 154) mentioned that the egg shell was rejected in pellet form some minutes after the egg's ingestion. He also gave the record of two specimens which during one year ate, between them, 124 pigeon's eggs.

Loveridge (1918, p. 331) noted that some lower spines penetrate the shells of the eggs, while Werner (1922, p. 385) wrote that only the first 24 vertebrae possessed hypapophyses, all directed anteriorly and penetrating the esophagus.

Loveridge mentioned *Dasypeltis* and remarked upon its habits in a number of papers. Among these are the following notes: (1928, p. 75) the species may eat the eggs of weaver birds; (1933, p. 245) in captivity a specimen ate a fresh egg, as well as two eggs that had been previously swallowed, and cracked but not broken, by another snake; (1935, p. 20; 1936, p. 256, pl. 4, fig. 1) the species is capable of a remarkable gape as demonstrated by a (posed) picture showing it with a hen's egg in its mouth; and (1946, p. 106) specimens will take only fresh eggs and will refuse incubated ones. In the latter account he also remarked that the normal diet of the species consists of entire clutches of small bird eggs, indicating that the snake stores up fat during the nesting (egg laying) season of the birds to last it through the dry seasons when eggs are more difficult to obtain.

Gadow (1933, p. 238), in discussing the evolution of the vertebral column, restated the fact that no enamel was present on the apices which crush the egg shell. With reference to penetration he felt that "such a permanent perforation by skeletal parts is very rare, the only analogous case being that of the sharply pointed ribs of the newt *Pleurodeles*." Rose in his unfortunately so ill-fated volume[3] "Veld and Vlei" (1929, p. 159), gave a brief treatment of the form together with a series of posed pictures of the egg-eating sequence.

In 1931 Haas published two papers on the jaw musculature and kinesis of the ophidian skull (1931, 1931a), in which the status of *Dasypeltis* was taken up in detail. He made a

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[3] The plates and a large number of bound copies were destroyed by fire shortly after publication.

number of discoveries in regard to the skull and also noted several previously unsuspected aspects of the musculature. Because of its fundamental importance, I shall return to one of these (1931a) when discussing the functional morphology of the head region.

F. W. FitzSimons in his work "Snakes" (1932, p. 121) again mentioned the sawing of the egg shell, this time also presenting a number of instances where these snakes succumbed by choking after swallowing eggs too large (turkey's egg) or too hard (china nest egg) to be successfully crushed. He stated that in the latter case the nest egg showed definite scratches caused by the heavily enamelled "bony saw." Hewitt (1937, p. 58) gave a general account of the egg-eating process, together with a picture (posed?).

Pitman in his excellently illustrated "Guide to the Snakes of Uganda" (1938, p. 124) unfortunately quoted F. W. FitzSimons' (1932) remarks on habits in toto. He also stated that thanks to two rainy seasons there is no winter in Uganda, allowing the specimens to be active twelve months out of the year with food available at all times.

Jürgens (1939, p. 551) presented posed photographs showing a specimen ingesting an enormous egg. His text repeats Ditmars' and F. W. FitzSimons' errors.

In a magnificently clear series of photographs published initially in Animal Kingdom (1945, pp. 188-189) and later (1946, p. 124) reprinted, Dunton presented what seems to be the first actual photographic record of the egg-ingestion sequence. Personal conversations with Mr. Dunton about these photographs have provided me with several details of the swallowing process.

V. FitzSimons (1946, p. 352) mentioned surprising a female specimen while it was ingesting an egg. Immediately after being captured the specimen disgorged the egg intact. Cansdale (1948, p. 46) discussed the feeding habits of the form, and Rose (1950, p. 248), in a revised and expanded version of his earlier (1929) volume, presented a variety of observations on the habits and egg-ingestion process of the form as well as the method of crushing, all of which will be taken up further on.

Gans & Oshima (1952, p. 11), referring to Kathariner as well as to unpublished observations by Benzer, definitely refuted the presence of enamel on any of the hypapophyses.

## Habits

*Food Recognition and Food.*—While it may appear to be almost axiomatic that eggs form the exclusive diet of adult specimens of *Dasypeltis*, the problem of food recognition has received considerable attention in the literature. Its interest, as pointed out by a number of authors, lies in the fact that snakes generally feed on moving prey. Haas (1931a, p. 373) remarked on this and wondered about the method by which a juvenile snake initially recognized the egg, putting forward the possibility that it might be attracted to it by the behavior of the brooding hens.

Food recognition among the Ophidia appears to depend mainly on visual (Wiedemann, 1932, p. 282) and olfactory (Wilde, 1938, p. 445) clues, although vibrational (Mell, p. 236) and thermal (Noble & Schmidt, 1937, p. 263) stimulations also play their part. Visual recognition seems to be restricted to moving objects, and there is no reason to assume that vibrational or thermal clues play any part in the recognition of this specialized food. Hence only olfactory clues remain to be considered. Their use was recognized by Durham (1896, p. 715), who mentioned that the specimen examined the eggs with its tongue prior to its attempt at ingestion, and by F. W. FitzSimons (1912, p. 106), who stated that the eggs are recognized by smell and presented considerable evidence to substantiate this belief.

This leads us to the types and the condition of the food. Durham *(loc. cit.)* stated that she never knew her specimen (18.8" total length?) to take anything larger than a hedge sparrow's or canary's egg, although a specimen in the British Museum was stated to have been preserved with an ingested (and unbroken) hen's egg in its esophagus, and Vaillant (1899, p. 97) mentioned a specimen caught and preserved in the act of eating a duck egg. F. W. FitzSimons (1912, p. 106) indicated that specimens would not take addled eggs or those with embryo birds. Neither would his specimens accept old, blown shells which had been refilled with fresh egg batter. He stated that these snakes probably also eat the young of birds, as well as various soft-bodied creatures such as lizards, worms and various larvae, without, however, presenting any evidence to confirm this somewhat startling hypothesis. Ditmars (1922, p. 276) referred to the ingestion of soft, leathery-shelled eggs of other species of serpents, and Loveridge mentioned the eggs of weaver birds (1928, p. 76), including those of the mannikin *(Spermestes c. scutatus;* 1933, p. 246).

In 1932 F. W. FitzSimons (p. 121) reported a number of items regarding the dietary habits of this form that were subsequently quoted by at least two other authors (Berridge, 1935, p.

69; Pitman, 1938, p. 127). All of them deal with specimens that "choked to death" when they tried to swallow eggs too large for them. The first two were eating turkey and duck eggs, while the last case concerned the aforementioned (see historical section) china nest egg. Even if the question of the relative hardness of porcelain and eburnified bone is avoided, these stories sound most strange in view of the well-known facility with which snakes generally, including *Dasypeltis* (V. FitzSimons, 1946, p. 352), manage to disgorge recently ingested, large and often unwieldy prey when disturbed.

Loveridge (1946, p. 106) also stated that this species will not take eggs that have been incubated, while Cansdale (1948, p. 46) reported that the specimens would probably take all varieties of eggs and not only those of birds. He mentioned the example of a large (three-foot) specimen which "was laying female and seemed to swallow each egg the day after she had laid it; but, of course, this was in a confined space and cannot be considered at all typical. Many other eggs are available, including the round, hard-shelled eggs of the giant snail, *Achatina variegatus* and those of many lizards and small snakes."

Finally Rose (1950, p. 258) definitely stated that specimens would accept partially incubated eggs, out of which they squeezed the liquid, rejecting the solids with the shell. He continued that the form would also accept addled eggs, but after swallowing and cracking, rejected them.

In analysing and attempting to evaluate the sometimes conflicting statements listed above, it seems probable that, as *Dasypeltis* recognizes its food almost exclusively by the use of the tongue-Jacobson's organ combination, the snake will reject eggs that smell unusual, whether they be blown ones filled with batter or addled ones in which decomposition has progressed sufficiently to be externally noticeable. There does, however, appear to be no reason for discounting Rose's statement (*op. cit.*) and photographs recording the fact that the species will eat eggs in varying stages of incubation. Surely a far greater proportion of nests examined at random will contain incubating eggs rather than fresh ones. Hence refusal to eat such partially incubated eggs would impose an unnecessary hardship upon the snake, robbing it of a large source of available food.

Once having started to feed, snakes will ingest subsequent food items indiscriminately until the supply stops, or the generally quite elastic maximum capacity for the particular specimen involved is reached. After the first ingestion they will grab at any object of the correct size, shape and odor, as is well known to anyone who ever attempted to feed fish to specimens of *Natrix*. This tends to explain Loveridge's experience with cracked eggs and perhaps also Rose's with addled eggs, though of course in the latter case the egg might not yet have reached the point where the odor of decomposition could be perceived through the shell. In any case it appears doubtful whether any snake used to eating entire clutches of eggs would make more than a cursory examination of any egg after the first. It might thus be quite possible that a specimen would ingest a china nest egg, but in view of the above-mentioned evidence it appears rather improbable that it should be unable to regurgitate.

We now come to a number of subjects, in regard to all of which we suffer from a complete lack of evidence. First is the matter of the use of non-avian eggs as food, as well as the food of juvenile specimens. In spite of Kathariner's speculations (1898, p. 518), based upon the presence of larger teeth in the mouth and "Hautfetzen" in the stomach of the juvenile, the only definite information on this point is given in Cansdale's above-quoted observation, admittedly made under abnormal conditions. Any further observations that may have been made have never found their way into the literature. Furthermore, with the exception of Pitman's remarks (1938, p. 129) regarding the year-round abundance of eggs in Uganda and Loveridge's statement (1946, p. 106) that specimens store up fat during the egg-laying season, there is no evidence indicating how this reptile manages to find food the year-round in such regions as South Africa. On this point as on the previous one field observation and further data on the habits of this snake will have to provide the answer.

*Feeding.*—As already indicated in the section on history, the actual observations of and comments on the feeding process are few, a fact which does not appear, however, to have deterred a number of people from writing expansively about the topic. This lack of actual data has been reflected in the divers aforementioned statements regarding food preferences and in the extreme variation in the descriptions of methods theoretically utilized for both ingestion and crushing. While a number of other authors, whose information (based upon analysis of specimens or the literature) is of interest, are also referred to here, the two studies from which most of the information here given was taken are Durham's 1896 (*loc. cit.*) paper and

Dunton's 1945 (p. 124)[4] series of photographs.

As described by Durham the swallowing proceeds as follows: After the preliminary investigatory period (I would consider the "feeble snap" mentioned to belong here) the specimen gaped widely, grabbed the egg by the smaller end and, "the jaws and the skin under them expanding enormously," swallowed the eggs with a "strong effort." If Dunton's photographs of the process are here consulted, some very amazing features may be noted. It will be seen that the mandibles and the labials seem to be entirely separated. The line of labials runs downward from the angle of the mouth to disappear beneath the egg (unfortunately no photographs of the ventral aspect of the snake at this stage of ingestion are available), while the mandibles are somewhat anterior to this line, apparently connected to it by little more than the membranous lining of the mouth. There appears relatively little deformation of the head, the only noticeable change being a slight widening toward the gape. Unfortunately, Durham's drawing of the swallowing process (pl. 32, fig. 2) did not indicate any motion of the scales relative to the mandible, perhaps because the small size of the egg ingested by her specimen did not make this too apparent.

Vaillant (1899, p. 97), in his figure of the snake mounted in the act of eating a duck's egg, shows this separation of labials from the mandible quite clearly, though since the specimen pictured had almost completed the engulfing act the gap shown is none too great. The thing that is clearly apparent in his picture, though not especially referred to in the text, is the special "lip" located at the center of the stretch of skin between the two mandibles and hence directly under the egg. It is made up of the anterior labials and chin shields, with the ventrals as a base, which appear to push the whole structure under the bottom of the egg. The morphology and function of this peculiar modification will be discussed in detail in the following sections. It should also be noted here that Ditmars (1912, p. 204), in discussing the ingestion of eggs in *Dasypeltis scaber,* mentioned that this was facilitated by a peculiar peristaltic motion of the muscles of the chin.

Durham states that after the egg has entered into the esophagus of the snake, the reptile remains still, with its head raised, the spine being strongly arched and the whole throat greatly extended. It next slowly lowers its head, with great effort "driving the spinal teeth into the egg and crushing it." The egg was then gradually flattened, the snake resuming its natural proportions about fifteen minutes after first seizing the egg. (Durham's statements as to the time required for the various portions of the performance must be doubted, unless the supposition is accepted that the snake retains the shell for 1½ hours after emptying it.) Dunton's illustrations clearly show the extreme curvature of the spine, as well as the considerable distention of the esophagus. They indicate that during the crushing period the egg has progressed to the point where its blunt end is located approximately 2½ times the width of the head from the tip of the snout. The photographs are clear enough to show the constricting effect of the throat muscles, closing the esophagus behind the egg.

After an extended period of rest Durham's specimen quite suddenly and violently began to press that portion of the body containing the crushed shell against the ground, simultaneously arching (in a vertical plane) the body behind it and raising its head. This action was repeated several times, the specimen meanwhile crawling about restlessly. After a period of time it raised its head, opened its mouth and with a violent lateral wriggle ejected the crushed shell. An unpublished photograph of Dunton's clearly shows this lateral wriggle, which in Durham's otherwise quite adequate sketches seems to have been transformed into a vertical undulation.

## MORPHOLOGY

The material to be covered in this section has been extended to a discussion of all those aspects of the snakes of this genus that are in any way connected with its specialized habit of egg-eating. Former evaluations of morphological modifications have mainly concentrated upon the vertebral hypapophyses and on the relatively reduced dentition. Only a few authors appear to have considered the possibility that additional modifications of other structures might also exist. Vaillant (1899), in the passage quoted above, inquired into the reason for the existence of modifications of the gums and speculated on their function, and Haas (1931a) presented an analysis of the rather aberrant muscle arrangement and kinetics of the skull. While various authors either pictured or mentioned the presence of the enlarged neural spines, there does not appear to have been any further comment on these, and the general opinion regarding other portions of the animal seems to have been

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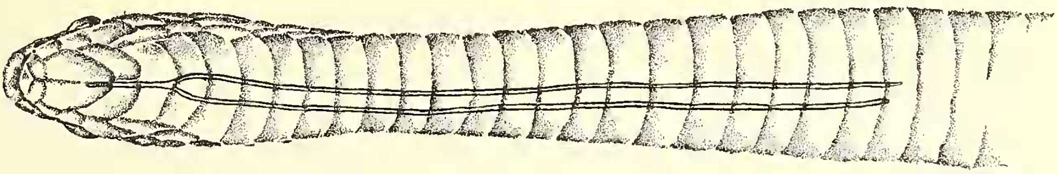
[4] Through the courtesy of Dr. James A. Oliver and Mr. Sam Dunton, both of the New York Zoological Society, I was able to examine the entire series of photographs taken, including several not published, and reference is to the entire pictorial sequence as reproduced here (Plates I-IV).



Text-fig. 1. Ventral view of specimen to show scutellation, with position of hyoid traced in for reference.

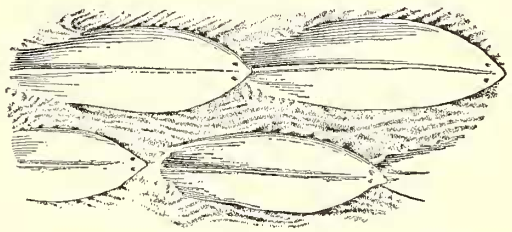
expressed by Gadow (1933, p. 283) when he referred to this "otherwise normal" snake.

*Anterior Lepidosis.*—When the anterior lepidosis of this form is examined, attention is directed to the concentration of scale rows in the cheek region and the absence of a mental groove, coupled with the almost total lack of true gular scales. The last two items are shared by *Dasypeltis* with only a very few other ophidian genera, and in combination with the first are sufficiently characteristic to allow immediate recognition of the genus.

In considering the first point it will be seen that three rows of dorsal scales (the sixth, seventh and eighth) appear to originate from behind the last upper labial. Those dorsal rows (the first through fifth), which in most colubrine snakes run into the gulars anteriorly, there being admitted beneath the chin by the reduction in width of the ventral scutes, here appear to squeeze into the region at and below the angle of the mouth. The crowding effect is enhanced further by the fact that the number of scale rows on the neck exceeds even the number of mid-body rows. Since the circumference of the neck is somewhat less than that of the body (as is usual in snakes), the average size of the dorsal scales of the neck is much smaller than the size of the corresponding scales at mid-body.

The integument of the chin (Text-fig. 1) differs drastically from that of most other forms because of the above-mentioned absence of a mental groove. The mental scale is short, but broad, covering the entire frontal aspect of the jaw. The first pair of lower labials joins at the mid-line, being followed here by two pairs of chin shields. The forward edge of the more anterior pair is concave, and the rear of the two scales forms a partial ellipse whose long axis is on the snake's mid-line. In some specimens this ellipse has been modified into an equilateral triangle with rounded corners. The second pair of chin shields is smaller again, rounded posteriorly, and abuts against and encompasses the posterior region of the first pair. The first ventral scute is generally strongly curved, being concave anteriorly and convex posteriorly. This marked degree of curvature is gradually dissipated in the following ventrals. There appears to be but one pair of gular scales, which in this case is modified from the first row of dorsals. This pair consists of one elongated scale on each side of the chin, adjacent to the ventrals and reaching from the second pair of chin shields to the second ventral.

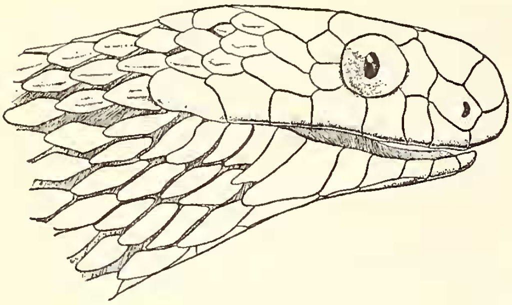
By stretching the gular region and examining it under low magnification (Text-fig. 2) the peculiar structure of the skin may be noted. The individual scales are found to be mounted rather centrally, as on a pedestal, their edges being entirely free. Between the rows of scales the skin is arranged in a pattern of fine folds and striations, indicating that a considerable amount of expansion can take place here. All of the above folds, including those of the skin between scales in the same row, proceed in parallel with the main axis of the animal. The attachment of the enlarged last upper labial is particularly noteworthy. Here almost the entire distal third of the scale is free, the folds of the skin curving beneath it and entering the angle of the mouth, thus producing the illusion that several of the scale rows end here.



Text-fig. 2. Detail of dorsal scale rows at side of neck.

The junctures between the chin scales differ from the above in that they appear to be tightly joined, with little or no room for motion relative to each other. The group of scales thus connected consists of the mental, the first four labials on each side, the two pairs of chin shields and the ventrals. The fifth pair of labials, the pair of gulars and the first row of dorsals adjoining the ventrals on each side, possess only a limited degree of freedom.

When the skin of the neck is stretched downward (Text-fig. 3) considerable relative motion



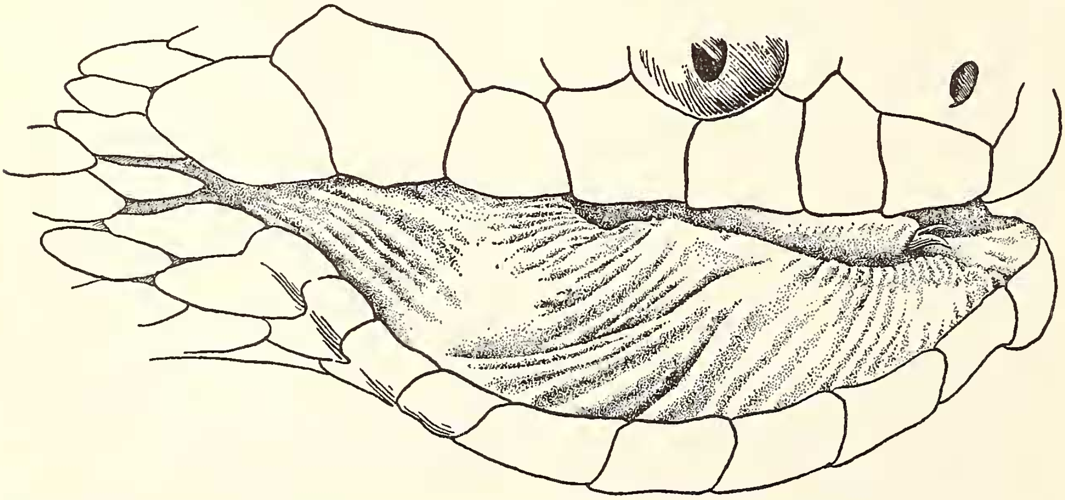
Text-fig. 3. Lateral view of head with neck skin pulled down to demonstrate arrangement of scale rows.

of the individual scales occurs and the scale arrangement at the side of the head and the neck becomes much easier to understand. The ninth row of dorsals, originating above the row of upper labials, retains its position. The slightly enlarged first scale of the next lower (eighth) row moves downward to the mid-point of the posteriormost upper labial. The sixth and fifth, fourth, third, second and first rows of dorsals connect respectively to the tenth, ninth, eighth, seventh, sixth and fifth lower labials, which thus become the anteriormost scales of these rows. It is to be noted that both the sixth and fifth rows of dorsals terminate in the tenth labial, the seventh row of dorsals moving down from behind the last upper labial to take up the position at the angle of the mouth. In the specimen depicted (Text-fig. 3) there is also one extra scale in the second row, and other similar variations of a minor nature have been noted in various specimens. None of these variations has, however, seriously affected the pattern described.

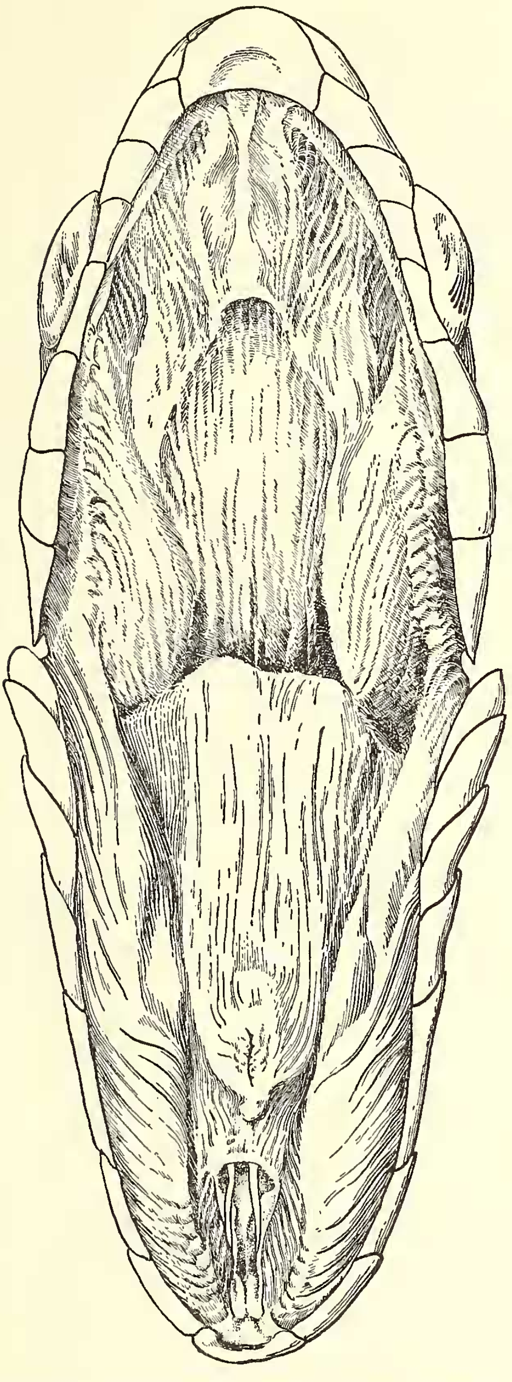
It may also be seen that a bi-axial system of organization exists in this region, the scales being roughly lined up in two directions. Here, too, the skin is very finely folded and the consequent expansibility between individual scales in the same row is high. Upon maximum expansion of the gular region these scales will, therefore, stand out individually, separated from the rows superior and inferior to them, as well as from the scales anterior and posterior to them in the same row.

*Interior of the Mouth.*—If the lip is pulled down to show the lateral aspect of the mandible (Text-fig. 4), the exposed gums are found to be arranged in innumerable finely wrinkled folds, plicated into one or two larger folds. These fine plicae run from the edge of the dentary rearward and outward, terminating on the edge of the five posterior labials. As already mentioned by Vaillant (1899, *loc. cit.*), these form a very deep and expansible crease between the labials and the mandible, allowing the one to be moved independently of the other. The fine folds cross the two mandibles and thence pass inward and rearward (Text-fig. 5) toward the mid-line, where they run next to those of the skin covering the median structures on the floor of the mouth (lingual sheath and trachea), the lines of expansion here being almost completely parallel to the long axis of the head. Posteriorly these folds continue right on into the expansile plicae lining the esophagus.

The ridges on the lower jaw, formed by the tissues crossing the dentary, exhibit a deep rearward folding, in some cases (particularly in large specimens) augmented by a mass of soft spongy tissue padding the anterior aspect of the dentary, as well as by a thickening of the covering membrane itself. The few teeth present



Text-fig. 4. Lateral view of head with lower lip pulled down to show structure of gums.



Text-fig. 5. Frontal aspect of gaping specimen.

in the posterior portion of this bone are often almost completely hidden by this tissue, but can always be felt.

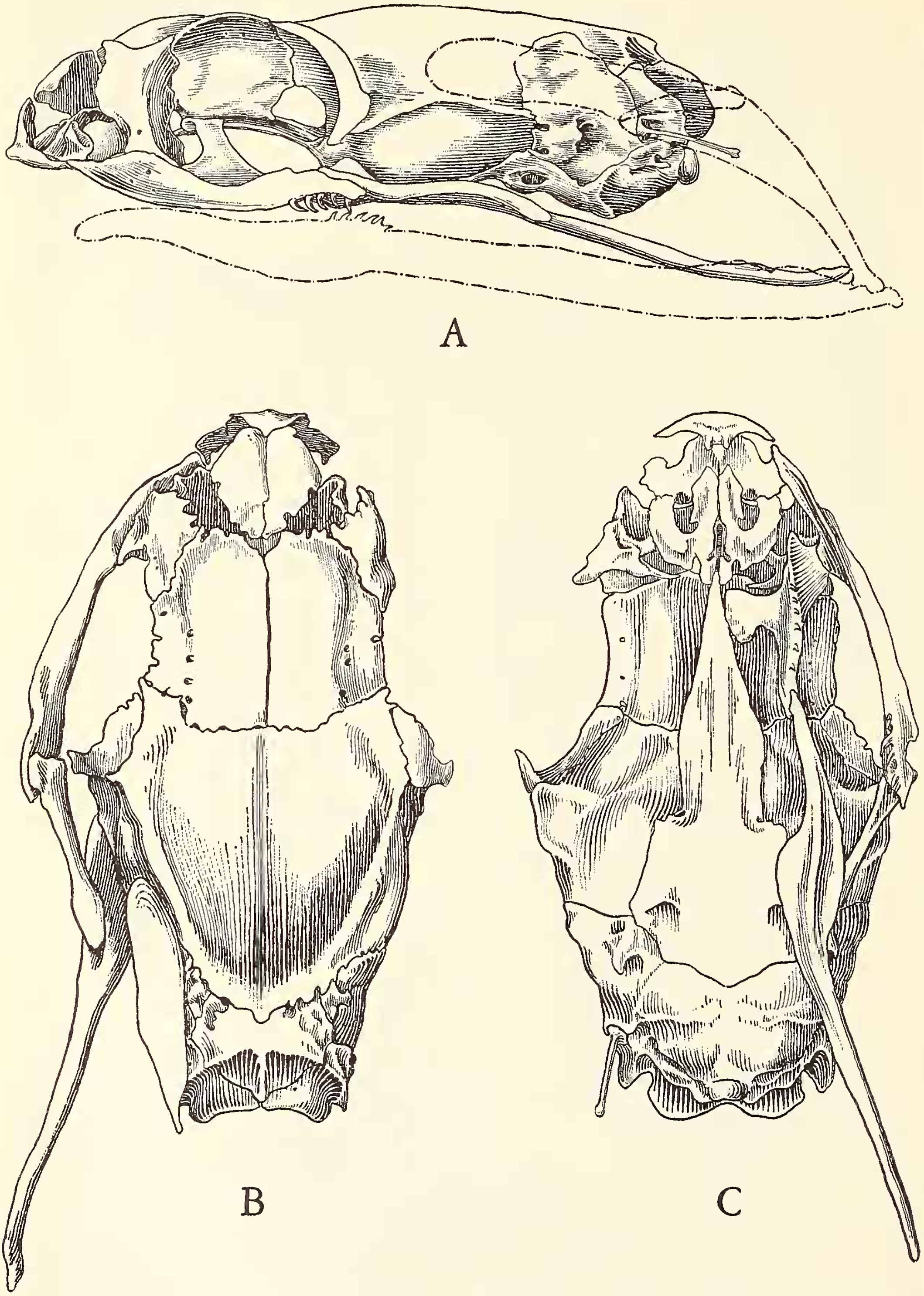
The rearmost portion of the mandible receives the attachments of the main muscles (*M. retractor mandibularis*), which sweep first backward and then upward and backward to the dorsal aspect of the skull. These muscles are also covered by a membrane folded so as to allow considerable expansion. While this sheet of muscular tissue restricts the opening toward the rear of the jaw, the lips pass beyond this point, the cut-off being located at about the seventh labial (see Text-fig. 4).

In the roof of the mouth, a very pronounced lip formed by the upper labials will be noted. Medially these labials also form a shelf which is tied closely to the clearly apparent maxillae by means of a membrane. The shelf of tissue and the internal membrane exhibit virtually no folding, indicating that the labial edges possess only a limited degree of motion relative to the maxillae. On the posterior portion of the latter, two to four teeth are generally apparent, although there exists considerable variation in both number and prominence of these visible teeth. Anterior to the toothed portion, the maxillae appear as long and relatively sharp ridges. These form an uninterrupted, inverted U together with the flattened premaxilla, which is covered by a down-folding of the rostral.

The twin anterior tips of the grooves, into which the ducts running to the organ of Jacobson open, almost touch the rostral. The remainder of the roof of the mouth located between the two maxillae presents a fairly normal appearance. Its main distinguishing feature is the complete absence of penetrating palatine teeth, which though present in reduced form along almost the entire length of the bone, are generally completely covered by the mucosa.

*Skull and Hyoid.*—Boulenger (1894, p. 354) figured the skull quite accurately though somewhat schematically and Haas (1931a) illustrated some of its elements. In discussing the kinetics of the skull the latter also mentioned various aberrant aspects thereof. He noted the peculiar shifting of the upper quadrate joint and the rounded ends of the pterygoids and remarked on the entirely strange aspect of the maxilla.

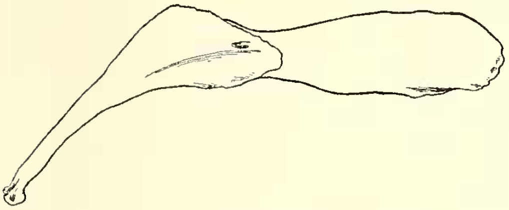
Text-fig. 6 shows several views of an adult skull. As pointed out by Haas, relative motion of the various elements of the brain case is almost non-existent. The fronto-parietal articulation is tightly bound, and shows in younger and juvenile specimens a certain amount of interdigitation. The same type of serration may also be observed on the anterior free edges of the frontal and prefrontal as well as on the posterior edges of the nasal. This interdigitation was present though in a varying degree in even the largest specimens whose skulls were examined. There appears to be some variation in the de-



Text-fig. 6. Views of the skull. The palatal elements of the right side have been removed to allow unobstructed view of ventral aspect of skull. A, lateral view, with positions of squamosal, quadrate and mandible indicated in dotted lines. B, dorsal view. C, ventral view.

gree of closure of the interval between the nasals and frontal as well as of the extent of this contact, but it has not yet proved possible to determine whether any constant differences in this regard exist between the various forms of the group. In general there is an inverse relationship between the degree of contact, or rather the strength of the articulation, of the various bones of the head (frontal, parietal, supra-occipital, basi-occipital, etc.), and the amount of serration or interdigitation noted.

The lateral half of the frontal above each eye is sharply bent upwards along a curved line which is perforated by a series of foramina. In some specimens this fold is continued onto the anterior portion of the parietal, where it runs outward to the parieto-postfrontal suture. The postfrontal is present in all specimens, its upper portion showing a varying degree of attachment to both frontal and parietal. The median suture of the nasals and part of the median suture of the frontals is sunk in a deep groove.



Text-fig. 7. Lateral view of the articulated quadrate-squamosal element.

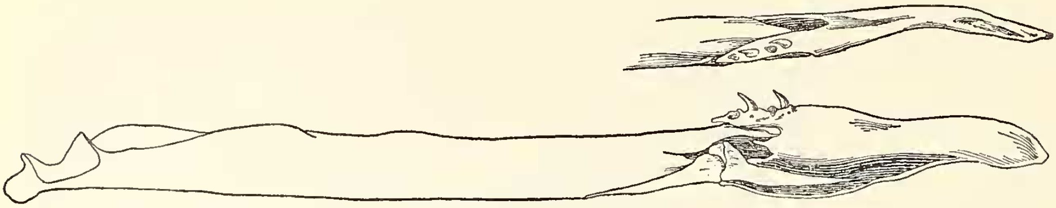
The parieto-squamosal (supra-temporal) articulation is very movable; however, the quadrato-squamosal articulation is particularly immobile, this being especially true in large specimens. The tightness of this junction was demonstrated in one of the skulls prepared, by a fracture during preparation of the head of the quadrate, which left a portion of this bone adhering to the squamosal. Even in the more juvenile specimens, where no such tight adherence is present, the degree of motion is very much restricted by the extensive articular surfaces (Text-fig. 7) of these two bones, formed by the extremely wide and flat head of the quadrate attaching to the flat and elongate squamosal.

The lower end of the quadrate articulates with the rod-shaped posterior portion of the pterygoid as well as with the mandible. The shape of the posterior pterygoid indicates that this bone is not built to withstand any sizeable bending stresses, differing in this respect from the pterygoids of a large number of boid, colubrid, elapid, viperid, and crotalid skulls examined. Anteriorly the pterygoid turns inward, flattening out somewhat and ending in a loose connection with the palatine. The anterior portion of the palatine articulates with a medial process of the maxilla, an articulation which is particularly strong in adult specimens. The wing-shaped process which runs from the upper portion of the palatine medially to the anterior section of the parasphenoid ridge is in this form much wider than normal, seeming to function as a further factor in stabilizing the palatine. The ectopterygoid or transverse bone lies in its normal position between the mid-point of the pterygoid and the posterior end of the maxilla, though the tight attachment of the latter bone to premaxilla, prefrontal and palatine and the particular lack of rigidity of the ectopterygoid indicate that it does not serve its usual function of moving the maxilla outward during ingestion.

The premaxilla is rather large and the entire vomero-nasal region is heavily ossified, in contrast to the posterior regions of the skull already described.

Both the maxillae and the palatines carry teeth, but despite Peters' statement (1882, p. 119), no teeth were found on the pterygoid nor has any other reference been made to their occurrence. Accurate counting of teeth was found to be extremely difficult. Even where cleaned skulls were used, considerable judgment was involved, as the sockets were irregular in both size and distribution. Boulenger (1894, p. 355) mentioned the presence of between three and seven maxillary teeth, and Bogert (1940, pp. 85-86) counted six to nine. The counts made by me fall within this composite range. Maxillary teeth varied from five to nine; palatine teeth from four to eight; and dentary teeth from four to five.

The anterior portion of the maxilla is quite unlike the shape of this bone in unspecialized species of colubrine snakes. It is only the posterior portion that bears any teeth, the anterior segment having a sharp inferior edge. The maxillae form a raised ridge defining the outer edge of the upper jaw, and meeting anteriorly with the lateral extremities of the heavy, centrally flattened premaxilla. The palatines are almost entirely toothed along their central section, although this dentition is very much reduced in size. The anterior edges of the palatines show the same sharp ridging that characterizes the maxilla. As is usual in many snakes, they are raised above the level of the upper palate, so that the maxillae will touch first when the animal bites a flat object, though this development seems somewhat more pronounced in this form. The premaxilla is practically immobile, while the maxilla is capable of only a very limited



Text-fig. 8. Views of the mandible. A, median view. B, dorsal view of tip.

degree of motion. The degree of freedom of the ectopterygoid and pterygoid is relatively greater, increasing in the order listed, but is still considerably below that usual to the elements of the normal colubrine skull.

The appearance of the mandible (Text-fig. 8) is peculiar both because of its proportions and because of the extremely weak articulation between the compound bone and the dentary. The former (composed of fused pre-articular, surangular and articular) makes up approximately two-thirds of the length of the mandible, is relatively weak, and its posterior groove for the attachment of muscles is quite short.

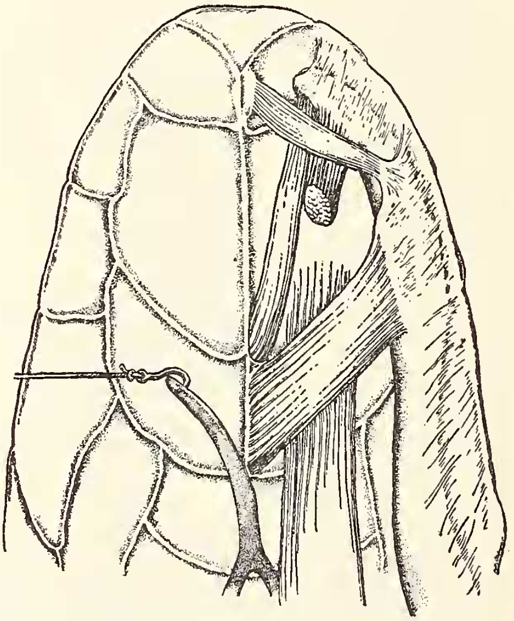
The compound bone shows an intricate but not very tight connection with the dentary, forming a functional articulation. Both angular and splenial are reduced to short triangular slivers of bone loosely attached to the two main members. A small bone in the joint, which appears alternately to fuse with the angular and compound bone, may be the very much reduced coronoid. The joint permits rotational motion about two main axes: a rather limited rotation about the long axis (up to a maximum of 30°) and an equivalent displacement about a vertical axis intersecting the long axis at right angles (bending). These become easily apparent if the mandibles are freed of the skin and superficial tissues and are bent or twisted. It may then be seen that the angular-splenial combination tends to limit inward displacement of the dentary, thus producing an important reinforcing action disproportionate to their size.

The posterior end of the dentary carries a few vestigial teeth; however, anteriorly this bone exhibits the same kind of a sharp ridge demonstrated by the maxilla. Furthermore, the height–width ratio of this bone (Text-fig. 8B) is quite large, so that the structural properties would show a decided change with difference in its orientation.

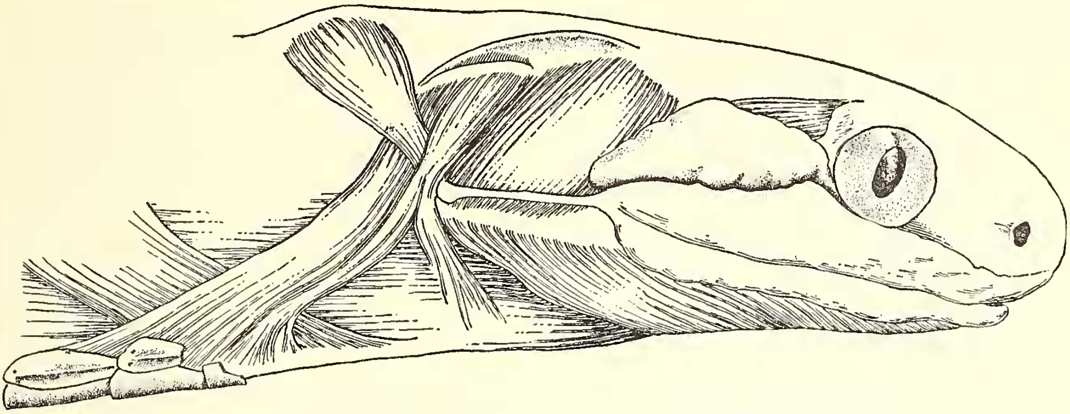
The hyoid is long, its posterior horns running back to between the eighteenth and twenty-second ventrals. Its shape is clearly shown in Text-figs. 1 and 9, and the tip of the glosso-hyal lies free underneath the epiglottis, while posteriorly the single element forks and is tied fairly closely to the skin at the rear of the throat.

Haas (1931a, p. 376) stated that the degree of freedom of the elements of the juvenile skull differed from that of the adult in being closer to that of a normal colubrid. This was confirmed by my preparations. The maxillae appear to be more loosely tied at both the prefrontal and premaxillary joints and the quadrato-squamosal articulation is capable of considerable motion. In one specimen part of the head of the quadrate was still cartilaginous, exhibiting as yet incomplete ossification of this cartilage bone, and the articulation was consequently very loose. A definite increase in the tightness of this connection as well as of the several other articulations was observed with increase in size.

Kathariner (1898, p. 512) made the statement that the dentition of his juvenile specimen was more strongly developed than that of his two larger specimens. Neither Haas's nor my observations offer any evidence in support of this. While a high degree of variation between



Text-fig. 9. Dorsal view of chin musculature.



TEXT-FIG. 10. Lateral view of head and neck with skin removed to show relative position of muscles. (Modified after Haas).

individual specimens was noted, it has thus far proved impossible to correlate this with size.

*Head Muscles and Harderian Gland.*—Haas (1931a) described the musculature of the upper jaw and skull in considerable detail. For this reason I shall refer only to certain muscles of the lower jaw not discussed by him, as well as to one group of muscles whose function during the engulfing process appears to have been insufficiently understood in the past.

The unusually strong development of the *M. retractor quadrati* has already been mentioned by Haas (see also Text-fig. 10). This muscle moves backwards and downwards from the head of the quadrate and ends in fan-shaped insertions in the skin lateral to the throat. Haas also speculated on its function, suggesting that a portion of it might represent the *Sphincter colli.* Dissection proved that Haas's drawing showed correctly the insertion of the posterior portion of this muscle on the lateral edges of the eighth and ninth ventrals. The anterior portions do not attach to the skin, but rather through the connective tissue between it and the wall of the esophagus. Certain of these anterior portions appear to be somewhat less strongly developed than was the case in Haas's specimens.

Text-fig. 9 gives a dorsal view of a dissection of the lower jaw which yielded some very interesting results. The tips of the two mandibles are entirely separate anteriorly and are not held together in any way. A pair of muscles runs from the lower surface of the dentaries' tips and attaches to the skin folds between the first pair of chin shields at their posteriormost point of junction. A second, larger pair of muscles appears to originate on the dentary just anterior to the joint between the dentary and the compound bone and proceeding much more laterally attaches to the raphe of the second pair of chin shields. A third pair of muscles acts in opposition to the last two, running forward from the mid-point of the dentaries and attaching to the raphe between the first pair of labials. This musculature of the lower jaw thus seems to be particularly modified to allow for the peculiar provisions for expansion observed in this animal. This matter will be discussed in detail in the section on Function.

In considering the morphology of the soft portions of the head of this genus, mention must be made of a peculiarly modified organ that is still insufficiently understood, although its presence was initially reported by Schlegel (1837, pp. 328-330). This is the gigantic Harderian gland, whose outline may be noted in Text-fig. 9. Haas, in discussing the muscles of the head, noted that certain muscles of the cheek region appeared to be arranged in such a manner as to allow complete emptying of this gland with maximum gape only. A further investigation of this phenomenon was reported and commented on in two papers. The first of these was the study of Smith & Bellairs (1947, p. 362) in which they showed that the main duct from the Harderian gland runs to the duct of Jacobson's organ in both lizards and snakes. Only a small side canal leads to the ophidian eye so that the contents of these large glands empty into the oral cavity. In the second paper Bellairs & Underwood (1951, p. 213) speculated that the secretion of this gland might in some way be related to the function of Jacobson's organ. While such relation may be possible in a large number of species, it seems hard to believe that this could be the function of this secretion in *Dasypeltis,* since any aid to the olfactory senses might be predicated to occur before rather than during and after the ingestion of the "prey."

*Alimentary Canal.*—As is usual in snakes, the lining of the esophagus is not differentiated significantly from the mucosa, the oral cavity thus gradually merging into the anterior esophagus. The plicae of the mucosa are continued here, resulting in a highly extensile anterior esophagus which extends back to within a very short distance of the heart. The posterior esophagus continues into the stomach, being but a narrow connecting tube. Although the lining of the anterior esophagus shows a profusion of folds, it adheres tightly to the muscles covering the bases of the vertebrae along the mid-dorsal line. In certain very large specimens this adherence has progressed to the point where the region of esophageal attachment to the mid-dorsal musculature is quite smooth, the normally apparent expansible esophageal tissue not starting laterally until the muscles overlying the rib attachments are reached.

The esophagus adheres to the sides of the anterior body cavity. This attachment proceeds approximately halfway down the length of the ribs. The remaining and ventral portion of the esophagus is even more expansible (to judge from the elastic folds) and is loosely suspended by connective tissue within the body cavity.

The most interesting aspect of the esophagus is demonstrated where it covers the projection of the various hypapophyses through the musculature. In discussing possible penetration in this region, it is of importance to make sure that such penetration was initially present, and was not produced by the scalpel of some previous investigator. Hence all statements regarding such penetration have been based upon the examination of previously unopened specimens (whether the opening had occurred for reasons of dissection or preservation).

It now becomes necessary to anticipate somewhat and to refer to the terminology utilized in the following section, where the anterior vertebrae of the vertebral column are divided into anterior, intermediate and posterior hypapophysials. For the sake of uniformity this regional terminology will also be utilized in referring to the esophagus.

This may be the best place to take up the puzzling question of osteological nomenclature involved in finding a proper term for the anterior group of vertebrae, characterized in *Dasypeltis* and many other genera by the presence of hypapophyses. The name *cervicals* would be inapplicable as the true cervicals, defined by the absence of ribs, are in snakes reduced to the atlas, axis and perhaps one or two additional vertebrae. Since such terms as *esophageal* and *thoracic* would either be difficult to define or have previously been defined differently, I intend to use the name *hypapophysial vertebrae*. These are here defined as those vertebrae of the precaudal series that carry hypapophyses.

Inasmuch as all the thoracic vertebrae of certain groups of snakes bear hypapophyses, the use of this term must furthermore be restricted to those snakes in which only the anterior section of the vertebral column is so developed. The term *hypapophysial* is, therefore, here used to redefine and replace Rochebrune's (1880, p. 552) term *thoracic* and Simpson's (1933, p. 2) term *anterior thoracic vertebrae*.

If the adhering esophagus of a large specimen is viewed *in situ* under a strong light, a series of short dark lines, coinciding with the location of the anterior and intermediate hypapophyses, becomes apparent. Kathariner (1898, p. 508), who prepared sections of the esophagus and the hypapophyses adjacent to it, stated that these "slits" in the underlying musculature continued through the esophagus, i.e., that in the adult animal the entire series of hypapophysials showed penetration of the esophagus. His juvenile specimen, however, did not have any penetration in either the anterior or the intermediate region. My findings agree in general with the above, though my much more extensive series shows a high amount of variation insofar as penetration is concerned.

In examining specimens under the microscope it was noted that the great majority of the slits seemed to be covered or closed off by a membrane or by what might best be described as an interior lip of tissue, and even the slight pressure of a blunt probe on the tissues surrounding the slit would often suffice to open it. For this reason the accuracy of any determination of the open or closed state of this slit is extremely dubious, the connection being so tenuous that rupture might occur even under the most careful procedural conditions. It may even be stated as a rule that the tenuousness of the tissue covering increases with age or size of specimen, from the juveniles which have this entire section still tightly closed to those adults in which some of the anterior and all of the intermediate hypapophyses appear to penetrate. While individual specimens of intermediate size show several types of variation from this, the above may be stated to hold true for the great mass of specimens examined.

In general the gape of these slits appears to conform to the size of the hypapophyses. The slits for the hypapophyses of the anterior region are elongate and narrow, and upon insertion of a probe the tissue will be found to separate from the bone in a like manner as the gum does from a tooth. This separation is found in the hypapophyses of all three series. In the intermediate group the tissue tends to spread wider and will allow complete penetration of the egg-shaped hypapophyses under pressure. Even when these intermediate hypapophyses are fully covered by tissue, their location may easily be noted, as they form definite lumps under the lining of the esophagus.

In the posterior hypapophysial region the appearance of the esophagus is entirely different. Here a series of five to nine spine-shaped hypapophyses are present and the majority of these effect permanent penetration. The esophagus bulges out over their tips to form a thick, cone-shaped mantle, through the apex of which penetration generally occurs, although this may occasionally proceed through the side. The anteriormost and posteriormost spines of the series, which are generally shorter than the remainder, may not penetrate at all, the mantle covering them completely. The distal end of the covering tube of tissue shows knobby sulcations and may be rather irregularly formed.

While penetration always appears to be present in the posterior hypapophysial series, even juvenile specimens exhibiting full development in this respect, this penetration often seems none too noticeable. The tissue mantle cloaking the tips is very elastic and with the exception of specimens that had obviously completed ingestion very recently, only a very small portion of the tip of the hypapophysis is visible through the covering mass of tissue. There is virtually no ontogenetic variation in this character. Out of the entire series of specimens whose esophagi were examined, only one extremely young individual (MCZ No. 48389; body length 205 mm, total length 244 mm) showed no penetration at all. In other small specimens it was occasionally found that only the anterior two or three of the spines showed definite penetration, while the more posterior ones were completely coverd, though of course clearly visible.

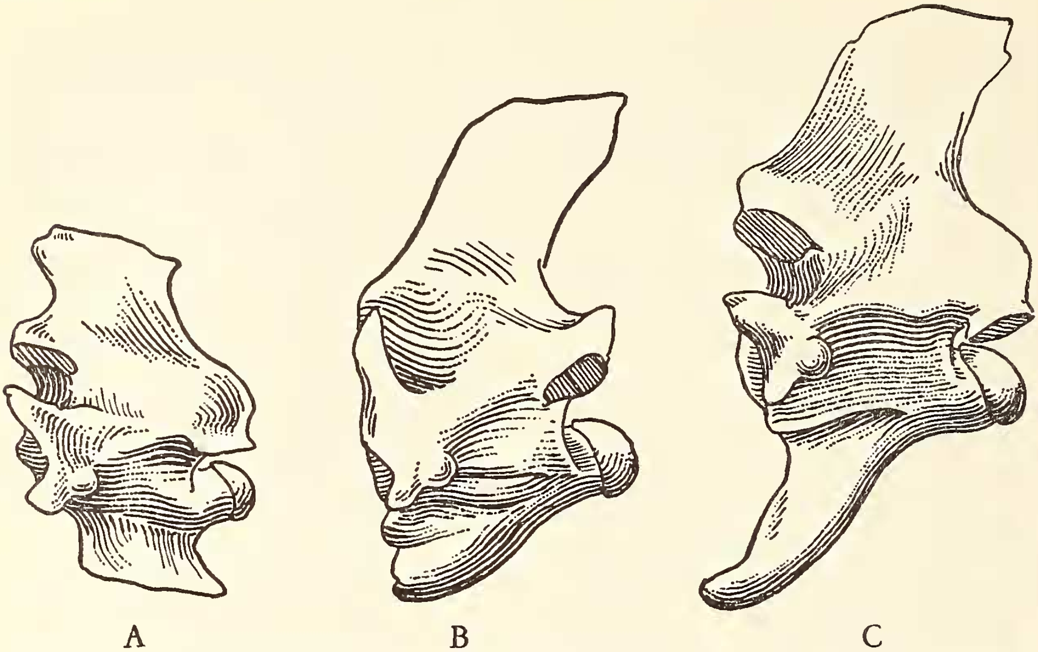
In examining the esophagi of large numbers of specimens a curious variation was noted that may well be related to the feeding cycle mentioned by Loveridge (1946, p. 106). In specimens in which the stomach was distended with yolk or those in which recently ingested yolk had been regurgitated into the esophagus during capture, the lips of the slits were pulled back and a large number of hypapophyses were exposed. In other possibly aestivating individuals the esophagus appeared quite shrunken and the number of exposed hypapophyses as well as the degree to which the slits were open was signally less.

The close attachment of the anterior esophagus to the muscles covering the bases of the vertebrae and lining the inside of the rib cage terminates immediately after the penetration of the last hypapophysis (or with the end of the hypapophysial series). It then rotates from its position in the apex of the roughly triangular body cavity, in which process it transforms into the very strongly constricted posterior esophagus.

While investigating this constriction Kathariner (1898, p. 509) found that the esophageal wall was surrounded here by a ring of smooth muscle fiber. This small tube, which shows infinitely less capacity for expansion than is exhibited by the anterior esophagus, bypasses the heart and ends in the stomach, which again possesses considerable capacity for expansion. The heart and the attendant constriction of the alimentary canal are generally located between the 32nd and 38th ventrals.

*Vertebral Column.*—In reading through the historical portion of the preceeding discussion it will be noted that most comments on the status of the egg-eating modifications of *Dasypeltis* have centered on the hypapophyses and on their penetration of the esophagus. These attracted general attention due to their supposed (though of course non-existent) relation to and compensation for the reduction of teeth in the jaws. The fact that they were considered to be "gular teeth" (note the names *Rachiodon* Jourdan, 1834, and *Deirodon* Owen, 1845) resulted in such errors as the assumption that the hard material capping them was enamel, and had the further unfortunate result of distracting general attention from other functionally significant modifications of the vertebrae and the attendant musculature.

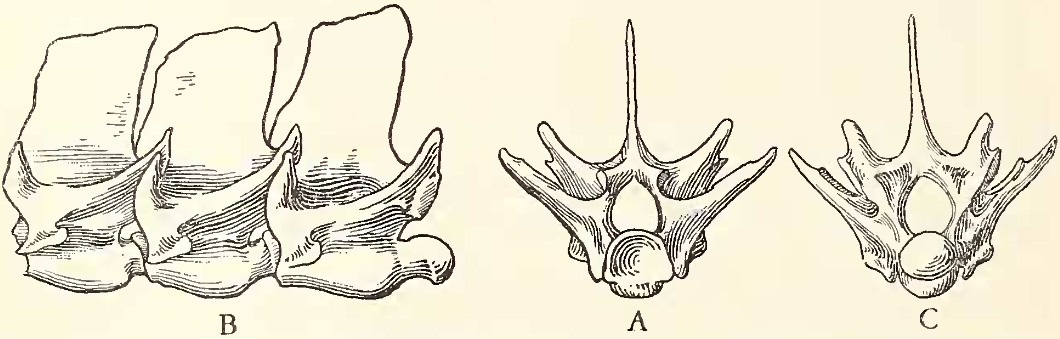
Since in *Dasypeltis* all vertebrae posterior to the atlas and axis bear ribs, the latter two constitute the only true cervicals. Not counting these, the next 29 to 34 vertebrae posterior to them carry hypapophyses, which exhibit a considerable amount of serial, ontogenetic, interracial and individual variation. This helps to explain the reasons for the diverse statements in the literature regarding the shape and appearance of these vertebrae. Owing to the variation in the hypapophysial series, it becomes of importance to establish a standard to which the others may be compared so that departures from the mode may be described. For this reason the first description will refer to the vertebral column of a selected individual used as a morphological type (MCZ 13232). The particular specimen described was used because it provided one of the largest and most highly developed skeletons at my disposal.



Text-fig. 11. Vertebrae of a fully developed adult specimen. Lateral views. A, anterior. B, transitional. C, posterior. For views of intermediate vertebrae, see Text-fig. 12.

Serial Variation: For the sake of convenience in describing the variation of the vertebrae and their hypapophyses, it becomes desirable tc divide these hypapophysials into three groups, hereafter referred to as anterior, intermediate and posterior. That this division is far from artificial will be seen from the subsequent section where it is demonstrated that each of these groups has a separate, well-defined function.

The anterior group is constituted by a series of vertebrae whose hypapophyses are relatively unmodified (Text-fig. 11A). They are all flattened and more or less rectangular, with only the inferior edge and part of the body of the hypapophysis thickened, and provided with a runner-like keel formed of a dense, very white and hard bone. There seem to be 17 or 18 of these vertebrae, the anterior four or five of which are directed somewhat posteriorly rather than straight downward. When viewed laterally the hypapophyses of the anterior series are of uniform height; however, they do become somewhat heavier as the intermediate series is approached and here there is also some strengthening of the keel, which may be slightly longer than the body of the hypapophysis. This produces the effect that the hypapophysis is concavely scalloped on its posterior and even on its



Text-fig. 12. Intermediate vertebrae of adult specimen to show maximal development of neural spines, aliform processes and zygapophyses. A, anterior view. B, lateral view of three articulated vertebrae. C, posterior view.

anterior edge, which character simplifies the problem of differentiating between the last anterior and the first intermediate hypapophysial. In making counts the first hypapophysis with straight, not undercut sides has been considered to start the intermediate series.

In those anterior vertebrae approaching the intermediate series the hypapophysis is inserted on a wide flattened keel on the ventral surface of the centrum. Thus the height of the actual hypapophysis is slightly reduced, but not the total distance from neural canal to the tip of the hypapophysis. In the first few vertebrae of the intermediate series the hypapophyses become very much thickened and reduced in height, appearing as a sausage-shaped, sometimes slightly ridged, elongate boss on the enlarged basal aspect of the centrum.

The last three to five (of a total of four to eight) intermediate vertebrae (Text-fig. 12) bear ovally rounded, egg-shaped lumps, which give the impression of having been formed by a compression deformation of the hypapophysis against the enlarged base of the vertebra.

There are usually one to two transitional hypapophyses (Text-fig. 11B) between the intermediate and the posterior series. The first one of these shows a slight lightening of the basal bulge, with a spine-like projection of varying height formed out of its anterior end. This is directed downward and forward at an angle of 60° from the axis of the vertebral column. This spine is of circular cross section, its diameter about twice that of the corresponding rib, and is distally rounded. The next hypapophysis in line either has the basal bulge greatly suppressed or totally eliminated.

The spines of the posterior hypapophysial series (Text-fig. 11C), which comprise six to nine vertebrae, generally show a slight bend midway up their length. This bend tends to turn the tips parallel to the column, thus pointing them more anteriorly. The last spine is often reduced in height and one or two of the terminal spines occasionally may be laterally displaced from the otherwise perfectly aligned series.

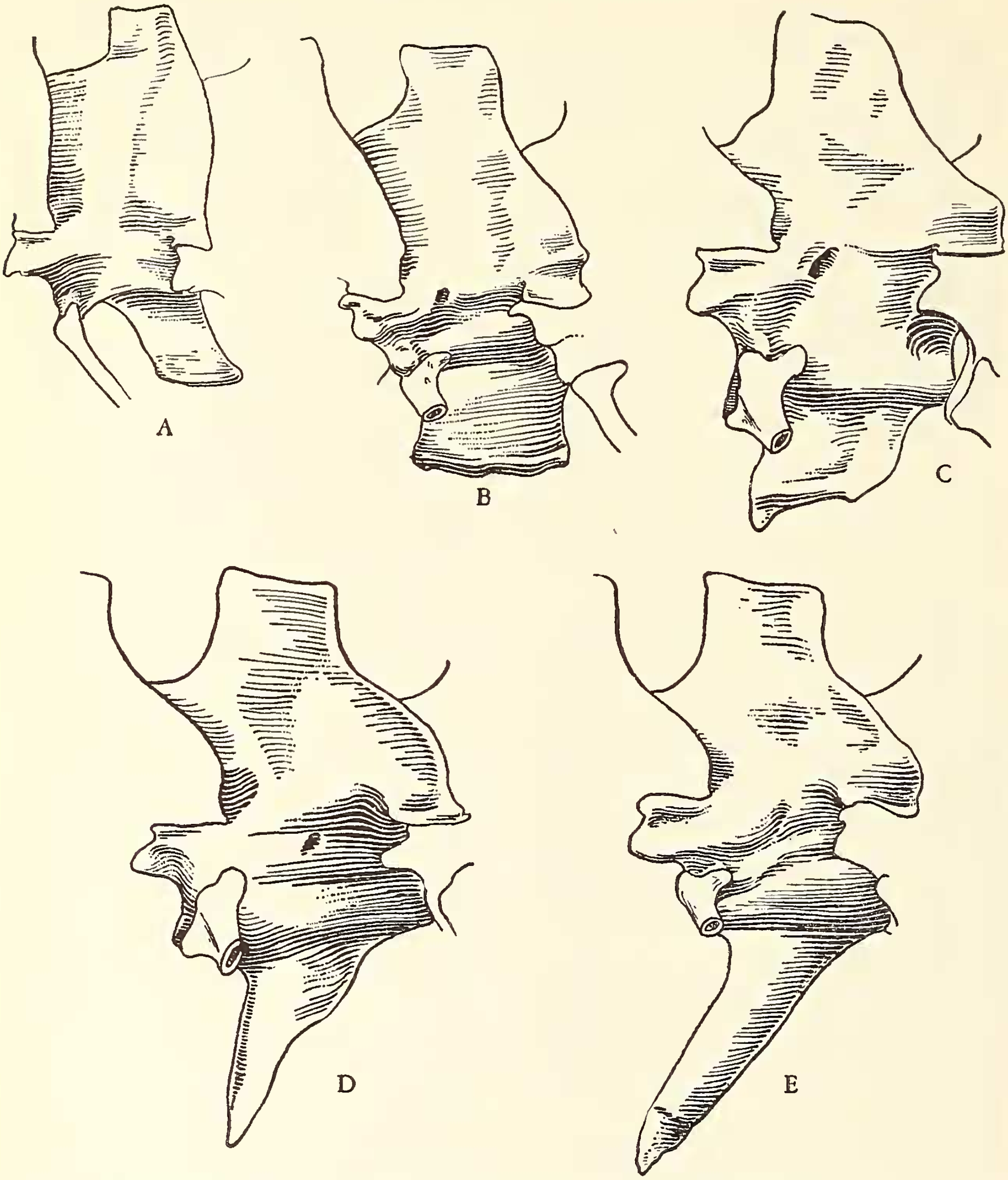
The neural spines of the hypapophysials also exhibit a serial variation. In the first few postcervicals they are roughly quadratic, slightly directed forward and approximately 5/4 the height of the corresponding hypapophyses. They increase in size along the entire anterior group, doubling in height with their length also increasing. Through the transition to the intermediate series and on the first few vertebrae thereof this increase is extremely rapid, reaching its maximum on the fully modified (egg-shaped) intermediate hypapophysials, where the height of the neural spine is more than twice the vertical dimension of the centrum-neural arch. In this region the width of these spines is sufficient to form an almost unbroken sheet of bone above the neural arch, which sheet is interrupted by only a very few insignificant spaces. The neural spines here are perfectly vertical, while those posterior to them show some backward inclination. The height of the neural spines declines even more sharply throughout the transition into the posterior hypapophysials. There is no further decline after the mid-posterior series. It is interesting that even where they attain maximum size these spines are extremely thin, by far thinner proportionally than those of specimens of comparable size in other species. It is consequently not surprising to note that captured specimens often show serious fractures of these spines in the anterior hypapophysial region, which further attests to their weakness.

The general aspect of the main portion of the posthypapophysial, thoracic vertebrae is that of a normal colubrid. The hypapophysials, however, show decided serial variation in this regard. This is correlated with the size of the neural spines and like these reaches a maximum in the intermediate region. One of these vertebrae exhibiting such a developmental peak is described here (Text-fig. 12).

The two basic dimensions of the centrum and neural arch are roughly equal. The pre- and postzygapophyses are directed outward and turn upwards at their ends. They give the impression that the centrum is considerably wider than high. Laterally and distally they are continued by elongate spiniform processes that are similar to aliform processes, but do not exactly fit Simpson's (1933, p. 3) definition. In an articulated series of vertebrae the posterior pair of processes will be aligned exactly above the anterior pair of the following vertebra. In cross section, the vertebra will thus have a very high, elongate and thin structure on its centerline (neural spine), which appears to rise out of a deep and wide bowl formed by the roof of the neural arch and the postzygapophyses with their extending aliform processes.

The articular facets are oval, unusually far extended laterally and extremely large. Particularly those of the postzygapophyses are raised on a blunt central pedestal. The articular surfaces are inclined 45° inward toward the neural spines and slightly downward posteriorly.

The zygosphene is fairly short, and projected shelf-like backward. The planes of the zygosphene-zygantrum articulation are even steeper than in ordinary colubrid snakes (where they are approximately 45°) and incline at 60° to



Tex-fig. 13. Vertebrae of a juvenile specimen drawn *in situ*. A, anterior. B, intermediate. C, transitional. D, posterior.

the horizontal. The condyle possesses an extraordinary degree of rearward projection and extends considerably beyond the body of the centrum. It articulates with an unusually deeply excavated cotyloid cavity, which is placed somewhat more posteriorly on the centrum than is normally the case. The implications of these rather divergent structures will be fully covered in the section on Function.

Ontogenetic Variation: It has already been pointed out in the section on the skull that in *Dasypeltis* there appears to exist a continuing development with age of the bony structure. This was also borne out for the vertebral column by the examination of a large series of juvenile and intermediate specimens.

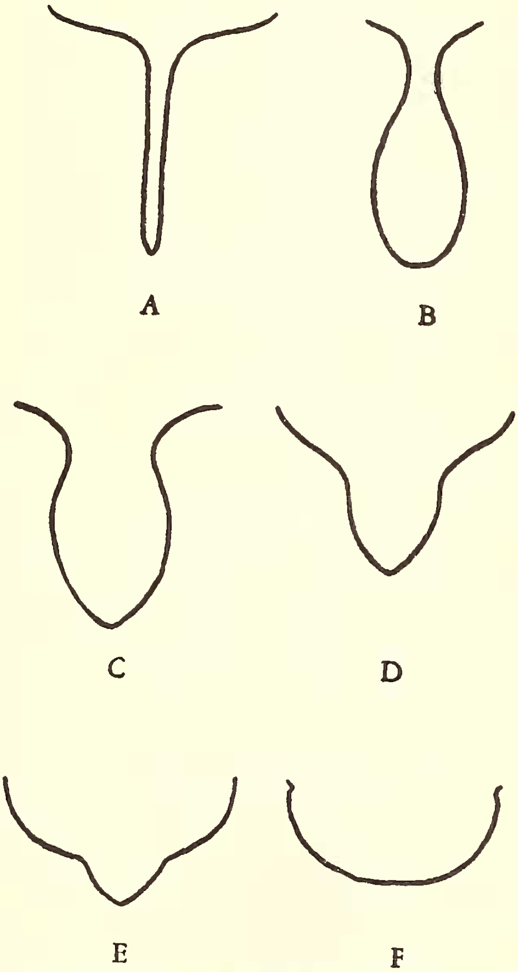
It is perhaps functionally rather significant that the major ontogenetic changes occur in the intermediate region, which generally exhibits far more variation than does the remainder of the vertebral column. Text-fig. 13 presents a series of vertebrae from an extremely small (and hence very young) specimen. Here it will be seen that with the exception of the somewhat smaller neural spines, the lack of keels on the hypapophyses and the as yet incomplete development of the posterior hypapophysial tips, both anterior and posterior vertebrae present the same appearance generally as do those of adults. It is furthermore simpler to correlate most of the differences exhibited in these groups with the increase in the size (and bulk) of the vertebrae, rather than with any more fundamental change in structure.

The vertebrae of the intermediate series of this juvenile are still so undifferentiated as barely to permit their being separated from those of the anterior hypapophysials. The neural spines are not yet enlarged and are of equal size throughout the hypapophysial series. The surfaces of articulation between pre- and postzygapophyses are still horizontal, and as yet only indications of the aliform processes are present. The hypapophyses are almost identical with those of the anterior series. They are square, slightly concave anteriorly, and show only slight traces of thickening on either body or keel. The posteriormost of the intermediate series (Text-fig. 13C, transitional), shows a slight anterior knob mounted on the square basic hypapophysis. This is of considerable interest as the appearance of this hypapophysis is very similar to that of certain anterior vertebrae of *Elaphe dione* (Pallas), another modified, egg-eating species presently being studied (Gans, MS.).

While there is a general correlation between vertebral bulk and degree of vertebral development in the series of specimens examined, the relation of vertebral bulk to total length of specimen varies considerably. It must furthermore be noted that different aspects of the vertebrae, such as hypapophyses, neural spines, aliform processes and zygapophyses, possess different developmental rates, with the growth stages of some of these processes not occurring simultaneously.

The hypapophysial development starts first and proceeds to completion most rapidly. Text-fig. 14 shows a schematic series of cross sectional views of intermediate hypapophyses, demonstrating the various stages of development from a plate-like structure in the juvenile, to an egg-shaped hypapophysis in the adult. Development proceeds through a thickening of the inferior edge (B), and a thickening of the body of the entire spine (C), to a fusion of the hypapophysis with the ventral platform of the centrum (D). In the last stage, just prior to completion of the developmental series, part of the hypapophysis is sometimes apparent as a central ridge or keel on the inferior aspect of the centrum (E). This doubtless explains Kathariner's statement that the intermediate hypapophyses were keeled in the adult and also the various functional interpretations based on this finding.

The other portions of the vertebra do not start to differentiate until the hypapophyses have reached stages C and D. Thereafter there occurs a gradual increase of the length of the neural spines and of the amount of lateral projection of the zygapophyses and their aliform processes. By the time the specimen reaches a snout-to-vent length of 500 mm, the hypapophyses have generally reached their point of maximum devel-



Text-fig. 14. Schematic sectional views of intermediate hypapophyses to show ontogenetic variation. A-F.

opment; however, it is after this point that the centrum reaches its maximal rate of increase in bulk and that the change in the arrangement of the zygapophyses takes place. For instance the centrum of a 700 mm specimen possesses almost three times the bulk of the centrum of a 500 mm specimen. Studies by Mr. Max K. Hecht (personal communication) on the vertebrae of rattlesnakes of the genus *Crotalus* have indicated that these continue to increase in bulk after the longitudinal growth of the specimen has slowed down or stopped. This seems to be correlated with an increase in the diameter and general bulk of the specimen, although it is to be questioned whether this proceeds proportionally.

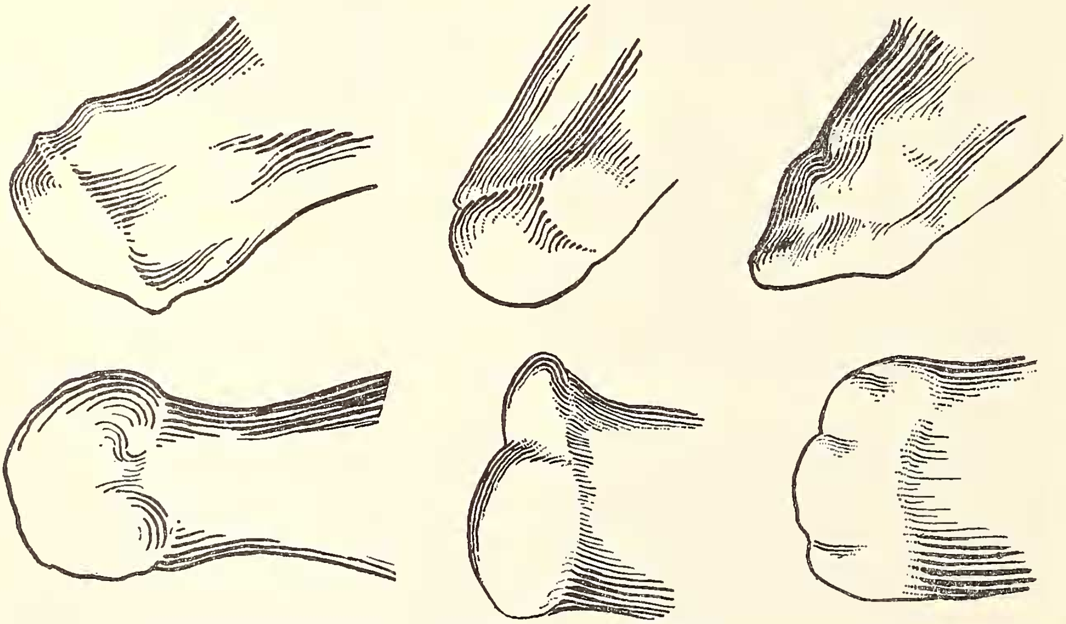
The increase in the size and arrangement of the zygapophyses, aliform processes and neural spines appears to occur simultaneously with this increase in bulk. This allows the assumption that these changes are related to the enlargement of the various dimensions of the hypapophysials, or rather that they form adaptive modifications to compensate for larger body size.

Inter-racial and Individual Variation: In examining large series of specimens, differences in the developmental rate of the intermediate hypapophysial series were noted, differences which seemed to be correlated with characters associated with certain as yet insufficiently understood subgeneric groupings. Since it is of course dangerous to base systematic conclusions on the evidence afforded by a single set of characters, the possibility of such inter-racial variation is only pointed out here. A rather astonishing amount of variation was also noted in the tips of the spinous hypapophyses of the posterior series though there exists no evidence to indicate that this possesses any inter-racial significance, particularly since various diverse types of tips have been found in a series from the same locality.

The "normal" tip shape is shown in Text-fig. 15A. Here the tip comes to a slightly bulbous point or is sometimes surmounted by a drop-shaped bulb of hard and dense, white bone. In certain other specimens this drop may be separated into a group of two to five separate drops which in their fused lateral arrangement create the appearance of a chisel-shaped tip, which may have a cuttting edge considerably wider than the diameter of the spine carrying it.

The shape of the chisel tips shows again a great deal of variation both between individual specimens and between individual tips of a single vertebral series. It can generally be stated that the two to four anterior tips are the ones that most often exhibit this variation, although further and more detailed generalizations must be omitted as unjustified in the face of such highly variable data.

*Ribs.*—Along the major sections of the vertebral column the articulation of the rib heads with the processes of the vertebrae is as de-



Text-fig. 15. Lateral and ventral views of the tips of posterior vertebrae to show individual variation. A, rounded. B, intermediate. C, full chisel shape.

scribed by Mosauer (1932, p. 193). Variations from this have occurred for only a few vertebrae, namely those of the intermediate group. Here the anterior-inferior parapophysial process does not show the usual rounded shape concordant with motion of the rib, but is almost completely flat, with a flat articulating surface also being shown by the corresponding portion of the rib head. The posterior-superior parapophysial process exhibits the usual rounded shape. An examination of the mechanism immediately makes it clear that this structural change severely restricts the motion of the rib, particularly in the dorsal direction. This may be easily confirmed by a tactile external examination of a preserved specimen in which the ribs of the intermediate hypapophysial region should refuse to bend inward, unless broken or disarticulated. This study of the rib heads was in fact undertaken to determine the reason for this stiffness, which had been noted during the initial examination of specimens prior to dissection.

*Axial Musculature.*—It is beyond the scope of this study to investigate the more detailed modifications of the muscles and muscle attachments of this form, when these differ from those of the colubrids described in Mosauer's studies (1931, 1935; Mosauer unfortunately did not include *Dasypeltis* among the genera investigated by him). Only major modifications, reference to which is basic to an understanding of the function of this form, are here considered.

In dissecting out the muscles of the anterior region it must again be noted that the skin is very loosely bound to the underlying tissues of the dorsal region and possesses a considerable degree of motility outward and downward from the dorsal mid-line. The two dorsal medial groups of muscles running above the vertebrae and laterally limited by the extension of the aliform processes are covered by an extremely strong fascia. The tendons attaching to the neural spines and to the lateral processes of the vertebrae originate from this fascia. The fascia is very much more strongly developed here than it is in such genera as *Elaphe, Ptyas* and *Natrix,* as well as in various members of the Elapidae and Colubridae examined for comparison.

In the region of the intermediate hypapophysial vertebrae the mass of median dorsal musculature is very strongly enlarged, the width of the two bands of muscles flanking the midline being expanded to fill the space provided by the widening of the vertebral base by the laterally spreading processes, and the increase in height of the neural spines. This increase in the size of the dorsal muscle is not paralleled by any corresponding increase of the ventral musculature. The general arrangement of these unusually heavy muscles would then tend to indicate that the snake should be able to straighten the (ventrally concave) vertebral column against a strong resisting force.

## FUNCTION

In developing a hypothesis regarding the function of the various modifications just described, it may be well to take them up in the order in which they are brought into play during an actual egg-ingestion sequence. The whole process may be divided into engulfing, cracking, crushing and ejecting.

*Engulfing.*—Various authors have remarked upon the swallowing ability of *Dasypeltis,* the genus in this respect even surpassing the not inconsiderable records set by other serpents. It is perhaps of even more interest to consider how an animal with the extreme mandibular and dentitional reduction exhibited by *Dasypeltis* manages to engulf food objects that are not only more than three times the diameter of its head, but are furthermore round, smooth and hard, almost appearing to have been designed expressly to make such swallowing extremely difficult.

Avian eggs are not an unusual dietary item of the Squamata. In fact it is probably true that most large snakes (and lizards) which normally feed on warm blooded prey will rob nests whenever the opportunity presents itself. In an earlier paper (Gans & Oshima, 1952, p. 13) reference was made to a number of methods utilized by snakes for crushing eggs, and it was pointed out that in the species mentioned (*Elaphe* spp.) egg-eating was practiced by the larger specimens only, so that eggs formed solely a supplemental dietary item. The adaptions described for several species of *Elaphe* brought eggs into the range of foods available to smaller specimens, but here the size relationship of specimen to egg was of an entirely different order from that demonstrated by even large specimens of *Dasypeltis.* It thus becomes apparent that the proportionately much greater "expansibility" present in the latter group serves to permit the initiation of egg-ingestion and the consequent exclusive egg diet at as early an age and as small a size as possible.

The ingestion method used by most snakes has been so often described in the literature as almost to obviate its restatement here. The specimen opens its mouth and bites the food object, thus engaging the recurved tooth rows on the maxillae, palatines and pterygoids, as well as those of the dentaries. In any and all of the motions that follow, the action is unilateral, the teeth of one member remaining set and providing a fixed point or fulcrum for the onward motion of the other member and of course vice versa. Neither side moves until the teeth of the other are solidly engaged. Since the food items are normally wider than the snake's head, sideways adjustment is required and has been provided by making the two quadrates capable of rotating around their attachment to the squamosal. In doing this they carry the posterior ends of the pterygoids (and the connected ectopterygoids, palatines and maxillae) outward with them. The mandibles, in swinging downward, simultaneously move out sideways, thus increasing the separation between the tips of the dentaries.

The integument covering the external aspects of the Ophidia seems admirably adapted for permitting such expansion. The individual scales are generally centrally mounted with their free edges covering and protecting the underlying skin, which provides the entire amount of flexibility of which the structure is capable. The mental groove, running from the tip of the chin into the gular region, appears to have the function of allowing the anterior chin region to expand without separating the labials from the mandible. Posteriorly where the enlarged chin shields run into the much smaller gulars, these serve to deflect the expansion laterally to the cheek region, where it is picked up by the skin between the dorsal scale rows.

The main disadvantage of the above method lies in the fact that the maximum height of the object swallowed may be but little more than the height of gape of the specimen. When this is exceeded by even a small amount the animal finds it extremely difficult to pull the unsupported skin (which is in considerable tension) over the inferior aspect of the prey. It might be supposed that snakes that swallow large animals by this method should have fairly heavy mandibles with sizable muscle insertions, built to permit the member both to receive and to transmit the forces and moments necessary to in this way pull the skin around the prey, and this is quite generally found to be the case.

In reasoning only from the fact that *Dasypeltis* eats very large eggs it would be theoretically correct to predicate an extremely heavy mandibular structure for this snake, a supposition that is, however, not borne out by observation. On the contrary, it is found (note the section on Morphology) that both the structure and the articulation of the anterior mandible are extremely fragile and that the latter is furthermore constructed in such a manner as to allow it to withstand sizable stresses in only one direction. For this reason the mandible has been provided with a hinge between the compound bone and the dentary. Since the diameter of the egg is considerably larger than the height of the gape, the method of ingestion must contain previously unreported factors that allow it to compensate for the lack of strong structure and permit it to exceed the ingestion limit imposed by the previously discussed method.

The answer to the above problem may be found by a consideration of the different character of the anterior lepidosis exhibited by this form. This indicates a high degree of specialization and proves that the complicated structural modifications serve to effect an extremely simple mechanical change. This ingenious modification consists of a change from a three-member to a four-member support for stretching the skin, "member" here being used in a mechanical rather than in an orthodox anatomical sense and denoting a structural element or a rigid part in kinetics. This change is thought to form a further specialization for egg-eating, as considerations below indicate that this particular mechanism would by its very nature fail with any prey of "non-egg" characteristics.

In discussing the ordinary feeding apparatus it does not seem necessary to take into consideration any special means of grasping. It appears self evident that this function is served by the teeth, admirably fitted both to grasp and and to anchor the body of the prey. When eggs are to be ingested, however, the effectiveness of these same teeth is markedly reduced. It is usual to observe slipping off and considerable maneuvering during egg-ingestion attempts by non-specialized egg-eating snakes. This normally continues until the specimen by accident or design manages to move the egg against a coil of the body or against a stationary object and succeeds in forcing its head over it. The main difficulty is due to the fact that the rigid structure of the toothed bones allows the egg to be touched by only a few teeth at a time. These few dental tips generally find insufficient traction on the rather smooth shell.

In endeavoring to explain how *Dasypeltis* has managed to overcome these manifold difficulties, and to determine the function of the modifications heretofore described, it appears best to retrace the steps previously listed for the ingestion sequence of a generalized colubrine snake and to consider the reasons for each individual deviation.

The initial gape of the specimen generally occurs in the same manner as in other forms. In *Dasypeltis* it is, however, enhanced by the fact that the effectiveness of the quadrate action has been increased by its close tie with the squamosal, and the squamosal's loose connection with the parietal. This results in a much longer member that rotates around the parietal attachment of the squamosal and allows the inferior end of the quadrate to swing further down and out than would be possible with normal attachment. In gaping the mandibles again rotate downward and outward around the extended distal ends of the quadrates.

As the quadrate moves outward it carries with it the posterior end of the pterygoid, which swings around the loose attachment of its anterior extremity to the palatine. The ectopterygoid tends to transmit some of this motion to the maxilla; however, due to the strong ties between this member and the palatine, prefrontal and premaxillary bones, little outward motion of its posterior extremity can take place in adult specimens. The palatine itself remains quite immobile, as the forces and moments imposed upon its posterior end by the rotating pterygoid's action upon the ectopterygoid are absorbed by the rigid junction with the maxilla and the prefrontal.

As the two mandibular tips start to separate, the critical difference between the engulfing act in *Dasypeltis* and the previously described sequence becomes apparent. Due to the absence of a mental groove, the expansion of the dermal tissues along this structure that permits such separation in almost all snakes[5] is impossible in *Dasypeltis*. In this form the mandibles, when swinging outward, leave the strongly joined group of chin shields unstretched between them. The finely folded mucosa, initially located between the mandibles and the lower labials (Text-fig. 5), then expands and with the muscles covered by it forms the only connection between the anterior mandibles and the median group of scales.

The purpose of this curious modification is noted immediately as the snake grasps the egg. At this time the entire group of chin shields, anterior labials and ventral scutes forms a stiffened band (possibly reinforced by the elongated hyoid) which is slid beneath the egg. This band is activated by the greatly enlarged *M. retractor quadrati* which inserts along both lateral edges of the eighth and ninth ventrals. As this muscle contracts (note Ditmars' 1912, p. 204 reference to "peristaltic motion" of the chin muscles) it moves the assembly forward, sliding it under the egg. This has the effect of reducing the tension in the bands connecting the chin scutellation to the mandibles, and releases these for further forward motion.

Dunton's figure 2 (1944, p. 189) shows the band of ventral scutes bent to an acute angle during the start of ingestion, which fact might be thought to negate the above statement that the chin scales receive any motion transmitted by these. Experiments with a metal measuring tape, whose structure is almost exactly analogous to that of the band discussed here, show, however, that such a tape will transmit forces and move around sharp bends, as long as the tape itself is sufficiently stiff and the radius of the turn is not too small. The marked degree of curvature apparent in the anterior ventrals, and the additional fact that every scale entirely encompasses the posterior aspect of the scale anterior to it, not only help to stiffen this structure but also provide admirably for the transmission of forces along the longitudinal axis of the snake. The ventral scales thus act as a fourth member during ingestion and allow the serpent greatly to exceed the ingestion limit that would be placed on a less specialized snake.

It might be reasonable to suppose that the above modification would have possessed considerable adaptive value in other species by increasing their gape and hence the diameter of prey that could successfully be handled. Consideration of the structural principles involved will, however, immediately show that the band would fail if a specimen should attempt to ingest any object other than an egg and of similar size, since the successful use of the modification depends upon exactly those attributes of eggs that make their ingestion difficult for unmodified forms. The hard and smooth surface and the absence of any projecting processes are essential, as the forces that may be exerted along the band of ventrals are very decidedly limited by the compressive strength of this stabilized column. For this reason four-member (upper jaw, mandibles and scale band) ingestion is definitely a modification whose adaptive value is limited to snakes that ingest eggs (or objects of similar shape) exclusively.

The elements of both the upper and the lower jaw of *Dasypeltis* are characterized by the absence of teeth on their anterior portions. Only a very few teeth, commonly referred to as vestigial, remain on the posterior end of these bones. In all specimens examined these teeth are, however, clearly apparent on both

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[5] A number of other genera of snakes (*Achalinus, Achalinopsis, Amblycephalus, etc.*) also lack a mental groove. It has not yet been determined whether this indicates similar specialization toward a wide gape or alternatively toward a reduction in gape. The latter might be permitted by or might even prove advantageous for a specialized diet of items such as earthworms (Pope, 1935, p. 186, for *Achalinus spinalis*) or snails and slugs (Dunn, 1941, p. 355, for *Sibon*).

maxillae and dentaries, though those on the latter were sometimes partially obscured by a fold of mucosa. Far from being vestigial, they serve a definite and important function. In discussing attempts at egg-ingestion of fully toothed specimens, it was mentioned that contact with the egg is managed by only a few teeth, these being insufficient to hold this "slippery" object. The change in the jaw structure of *Dasypeltis* appears designed to increase this contact. The reduced posterior teeth of the maxillae are small enough to take advantage of minor imperfections and the general roughness of the egg's surface. These teeth thus hook the egg, and the entire head of the snake rotates forward around this fulcrum so that the anterior, edentulous portions can also make contact. The protruding labial edges and the tissues covering the sharp-edged anterior maxillae, as well as the flattened premaxilla joining these, form a U-shaped band of soft tissue which, fitting around the curve of the shell, acts as a drag to any slippage or "outward" motion. Due to the shell's curvature, the palatines, which are recessed somewhat above the level of the maxillae, are able to make contact with the egg and their teeth increase the chance of a successful retention.

This might also be the best place to touch upon a possible function of the Harderian gland, which appears to be enormously enlarged in this snake. While it seems unlikely that its secretion is directly related to the function of Jacobson's organ, it may well serve as a lubricant or moistening agent to promote adhesion between the soft palate and the egg. Since the secretion would be required only during the actual ingestion sequence, i.e., when the specimen was gaping, the predication of such a function would tend to explain both the enlargement of the gland and the peculiar arrangement of muscles serving to empty it.

The structures above described mainly serve to maintain the *status quo* by holding the egg after it has once attained a certain position. Due to the very limited degree of motion possible to the adult maxilla, they are not capable of contributing much to the egg's actual ingestion. This is in direct contrast to the method previously described for a normal colubrid in which the two sets of maxillary teeth working alternately perform a large part of the function of drawing the head over the prey. Hence in *Dasypeltis* the weak and disproportionate-appearing mandibles are the members that, acting together with and against the upper jaw, contribute most toward moving the head over the egg, a feat for which remarkable seems too conservative a word. Text-fig. 8 shows that because of the considerable flattening of the dentary, this bone is unable to withstand a laterally applied force without deformation, although the channel-shaped element could transmit a sizeable vertical load. In order to maintain a firm grip on the egg, the snake must, therefore, keep these elements aligned at approximately right angles to the egg's surface.

A further reason why such orientation is of importance may be deduced from the special modifications of the tissues associated with the dentary that allow this member to grasp the egg much more firmly than can the maxilla. The posterior portion of the dentary is similar to the maxilla in carrying a few small teeth that here again serve to hook the surface imperfections of the egg. The anterior length of the bone is sharp-edged and crossed by large numbers of backward-pleated expansion folds of the mucosa, many of which are further proliferated into a mass of spongy tissue. This tissue acts in the same manner as the digital pads of many tree toads, or the finger tips of man. Such structures are able to build up very high static friction when they are pressed against even relatively smooth surfaces. Their effectiveness is furthermore directly proportional to the force exerted through them by the reinforcing bone, and hence to the "fit" of the bone to the egg shell, which fact again makes it imperative that the dentary be oriented correctly.

The articulation between the dentary and the compound bone is very loose, permitting both limited rotation and flexion. The attachment of the splenial and angular along the medial aspect of the joint effectively reduces the possibility that the dentary could be bent too far in this direction, and by reinforcing this bone permits it to withstand a moderate amount of medial tension. Forces of a much higher order can be carried in a vertical direction; however, any compression forces applied medially, or any tensile forces applied laterally, would cause rapid fracture of the dentary, the point of fracture probably being located quite close to the articulation with the compound bone. This structural weakness is compensated for by the fact that the muscles connecting the dentary to the ventral band of scutes appear designed to rotate this bone into the exact position in which it is capable of transmitting maximum force upon the egg. This means that the loose articulation between the dentary and the compound bone forms a functional joint. This does not seem to be the only example of such a joint in snakes, as has been recently pointed out again by Dunn (1951, p.

355) for the genera *Dipsas* and *Sibon,* in which genera the joint seems to be much more highly modified than is the case in *Dasypeltis.*

The dentaries are tied to the band of chin scales by three pairs of muscles (Text-fig. 9) which, upon being extended, will exert a medial tension on these members. As the snake grasps the egg and the chin shield assembly is forced underneath it, the connecting tissues and muscles will have to slide around the egg's diameter, thus being tangent to the shell at any given point. The force exerted on the dentary will, therefore, also be tangent to the egg and since the dentary is allowed a certain degree of rotation and orientation, it will tend to assume a position at right angles to the applied force and consequently at right angles to the shell. This remarkably simple mechanism assures correct orientation of the dentary during every part of the ingestion sequence.

Before passing on to the discussion of how the egg is cracked, there is a matter associated with the ingestion sequence that should be mentioned. The statement has repeatedly been made (Hoffman, 1890, p. 1544, *et. al.*) that the presence of teeth is a handicap in egg-eating and that their reduction in *Dasypeltis* possesses selective advantages by lowering the probability that the egg might be broken prior to its entry into the esophagus. Such remarks appear to be based upon inaccurate reasoning, as there seem to be no records of eggs having been broken during ingestion by any snake. If such an event does sometimes occur, it happens with sufficient rarity to warrant little consideration in this respect. As has been shown above, the dental reduction in *Dasypeltis* forms just one of an extremely complicated group of modifications, and alternate structures have arisen here to take the place of the teeth during ingestion.

Bogert & Oliver (1945, p. 356), in their discussion of dentitional variation in *Phyllorhynchus,* mentioned egg-eating habits as one of several factors possibly connected with this. It might seriously be questioned whether decided dentitional reduction would be an advantageous modification for snakes that specialize primarily on the soft-shelled eggs of lizards and snakes. This is particularly true where eggs form only a part of the diet, since a reduction in the number of teeth would definitely have a negative adaptive value insofar as the capture and ingestion of motile prey is concerned. It is possible, however, that a partial reduction of teeth might be advantageous in the ingestion of lizard and other soft-shelled eggs, since in this case there might exist the danger of ripping the egg shell with consequent loss of fluid during ingestion. Such reduction could occur by a decrease of average tooth size or by a decrease of the total number of teeth. Whether the disadvantages attendant upon such dentitional reduction would not tend to outweigh any advantages gained can probably not be answered for the general case and must bear further investigation for each of the forms involved. There still remains the possibility that separately incurred dentional reduction might have resulted in the elevation of lizard eggs to a food of primary importance.

*Cracking.*—The expansion folds between the dorsal scale rows allow these rows to separate widely as the egg passes into the snake's cheek region. Text-fig. 3 shows how the five posteriormost labials form the first scales of the various dorsal rows. As the ventral band of scales is somewhat retracted during ingestion, these labials are located almost vertically above one another on the expanded cheek region. At this point in the sequence the most striking thing about the appearance of the snake is the large and scale-less area of stretched expansive tissue that extends around the egg from the mandible to the ventral scutes.

The extremely loose attachment between the skin and the underlying tissues is very important because it allows the expansion to be distributed over the entire circumference of the animal rather than having it restricted solely to the skin of the lateral region. The strong ties of the integument along the mid-dorsal line serve only to prevent unilateral expansion, and do not in any way inhibit sideways slippage of the skin. It must be noted that this arrangement is not restricted to *Dasypeltis,* but is generally common to all snakes that feed on large prey, although differences in degree of dorso-lateral attachment seem to be present.

After the egg has been engulfed completely and is entering the anterior esophagus, the snake will be noted to be strongly bent, with the vertebral column deformed around the shell. It is at this point that the anterior vertebral hypapophyses perform their function. Rochebrune (1880, p. 553) stated that the hypapophyses in snakes are primarily concerned with "s'opposer à la régurgitation des aliments, pendant la déglutition et pendant les mouvements qui suivent l'ingestion de la proie." He obviously based this conclusion on the fact that these hypapophyses are directed posteriorly in most snakes. Examination of large series of alcoholic and skeletal specimens of a wide variety of snakes has not tended to confirm his hypothesis, however. Rather it is thought that these hypapophyses form a device that protects the bases and rib attachments of the anterior and generally smaller vertebrae from the direct pressure exerted by still struggling and often rather unwieldy prey. The presence of hypapophyses in the anterior region of the vertebral column of most groups of snakes may be related to the fact that here a high compressive force acts on the prey as the muscles of the anterior region assist the toothed elements of the oral cavity in pulling in and simultaneously stretching the prey. The selective advantage of this protective device is thus very much higher in the anterior than in the posterior region, where it would seem to possess no particular function. This lack of selective pressure is clearly demonstrated by the somewhat random occurrence of hypapophyses on the posterior precaudal vertebrae among the Serpentes.

In *Dasypeltis* the heads of the anterior hypapophyses are provided with a keel-like enlargement that permits the egg to slide over a series of smooth runners, thereby involving a minimum of effort for the muscles activating it. As these hypapophyses do not have the distal end protected by overlying muscles and are located with their heads directly beneath the very thin esophagus, occasional penetration would not be too astonishing. It is believed that the very tenuous tissue flaps over the heads of the hypapophyses may well be broken in the feeding season during which they are repeatedly crushed between two hard objects. In adult and very large specimens such perforation may even be permanent. However, in view of the highly variable nature of the available evidence, further speculation seems useless, and resolution of this not particularly important point will have to await the examination of large series of fresh specimens.

Few topics regarding this animal have been the subjects of so much conjecture as the method used for breaking the egg. Not only have such terms as crushing, piercing, cutting, bisecting and sawing been used with abandon, but these diverse functions have for one reason or another also been ascribed variously to the anterior, intermediate and posterior hypapophysials. Even Kathariner (1898), whose careful study decisively settled many morphological questions, was of the opinion that the ridged intermediate hypapophyses crushed the shell and he stated that the posterior spines served only to screen out fragments to allow their eventual ejection. Durham, who watched the actual sequence, correctly referred to the "driving of the spinal teeth" into the egg, but did not realize that at the point of her discussion at which this is mentioned the snake had already cracked the shell, and was obviously squeezing out the contents. The fracture of the shell is actually accomplished by means of a piercing action of the posterior spines, the exact method being described below.

As the egg reaches the region of the intermediate hypapophysials it will be noted that the main curvature of the vertebral column (concave ventrally) is reversed somewhat (convex ventrally) just posterior to the location of the egg in the esophagus. This projects the hypapophysial spines, often considerably flattened against the vertebral column, into the esophagus. Dunton's figure 5 also shows that the muscles of the neck region, including the anterior portions of the *M. retractor quadrati*, are strongly contracted, forcing the egg backwards against these spines of the posterior hypapophysials.

It might be well to introduce here several concepts customarily used in discussing the structural properties of materials. Among these are (1) the yield point, at which the deformation of a material under load changes from a state of elastic (reversible) to one of plastic (permanent) deformation, and (2) the ultimate strength, which indicates the minimum continuously applied force that could cause failure of the material tested. Both of these concepts, the numerical values for which would almost identical for any material as brittle as egg shell, are expressed in terms of stress (force per unit area). Owing to the fact that the ultimate strength does not vary for a given material at a given state, it can be seen that the force required to punch a hole through a uniform sheet will vary inversely with the diameter of the punch used. Since only that portion of the punch actually in contact with the sheet constitutes effective size, a sharply pointed or chisel-shaped punch would require a somewhat smaller force than would a punch bluntly rounded distally[6].

The requirement of a structurally perfect form, that a minimum amount of material encompassing a given space can withstand a maximum amount of imposed force, is met best by a sphere. Here all external forces are transmitted equally through the shell in all directions, and are hence distributed over the

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[6] It is realized that the above constitutes an oversimplification, since such factors as the cutting action of sharp-edged tools have not been considered here. In view of the rather primitive nature of the process involved, it is felt, however, that nothing would be gained by a more detailed analysis.

maximum area, which keeps the unit stress low. Once this balance has been broken by the appearance of even a tiny jagged hole, stresses tend to concentrate around its edges, resulting in the rapid spreading of "cracks" and the ultimate failure of the shell under forces whose magnitude is but a fraction of those withstood with impunity by an unpunctured sphere.

As the shell of an egg closely approximates the sphere structurally, the above statements may be profitably applied to the problem under consideration. Simple tests made with full size chicken eggs have confirmed this. It may be shown, for instance, that even though it is almost impossible to crush eggs between one's fingers, one can pierce their shells with pins or individual tines of a fork without appreciable effort. Thereafter any further imposed force, particularly if acting in the vicinity of the initial penetration, will crack the egg wide open.

Due to the sharp transition between the intermediate and posterior hypapophyses the egg suddenly "runs into" the projecting spines. The size of the tips is sufficiently small to allow penetration (piercing) to occur, activated by the force exerted by the contracting muscles of the neck. Once the first spines have penetrated the shell, the onward motion of the egg allows them to rip open the upper surface of the egg's posterior-facing extremity. As the spines are sufficiently long also to tear the shell membranes, this allows the egg's fluid contents to escape into the esophagus.

*Crushing.*—In the section dealing with the detailed morphology of this snake it was pointed out repeatedly that the maximum amount of difference of any of the hypapophysials from those of a normal snake is shown by the vertebrae of the intermediate series, and that these furthermore indicate a much greater degree of ontogenetic (and possibly also inter-racial) variation. These specializations are very extensive and even extend to the parapophysial rib attachments. This high degree of modification becomes easier to comprehend when the function of these vertebrae is considered in detail.

Inspection of the peculiar structure of the articulating processes and surfaces of these vertebrae (Text-fig. 12) and of the dorsal musculature associated with them immediately shows that what is involved are adaptations for extreme flexion of the vertebral column, as well as for the production of such flexion against sizeable opposing forces. Mosauer (1935, p. 82) gave 13° as the normal degree of ventral flexion and 12° to 18° as the normal amount of dorsal flexion for the mid-body vertebrae of the colubrid column. While measurement of values for the intermediate hypapophysials of *Dasypeltis* has proved impossible for a variety of reasons, simple inspection of Text-fig. 12 shows that these values are probably of an entirely different order here. Both the very wide neural spines, which would interfere with each other after only a few degrees of dorsal flexion, and the peculiar articulation of the extended condyle into the deeply excavated cotyloid cavity of the following vertebra, indicate clearly that little if any dorsal flexion can occur here. However, both the form of articulation of the ball and socket joint and the extremely large articulating surfaces on the zygapophyses indicate that no such limitation exists with reference to ventral flexion and that Mosauer's value for this may well be exceeded. The rib attachments are almost plane in this region, with the articular surfaces of the ribs being similarly shaped. This means that the ribs do not have their usual motility, as they extend laterally and are stiffly tied into this position. This probably serves to keep them from interfering with one another during the periods when the column is strongly bent. The fact that interference does constitute a danger can be fully appreciated only when Dunton's photographs are examined in detail.

Considerably less modification of this region would be necessary if the specializations had been designed solely to permit a high amount of ventral flexion. It is rather the additional complication of a strong force that makes these unusual changes necessary.

After the egg has been ripped open, the two wide bands of muscles flanking the dorsal midline start to contract, thus straightening the vertebral column. This contraction squeezes the egg, which is still fixed in position by the muscles of the neck, and crushing the previously cracked shell, starts the contents flowing toward the stomach. The enlarged neural spines of the vertebrae, together with the saucer-shaped troughs formed by the neural arch and the wide zygapophyses, provide adequate attachment and bearing surfaces for the relatively enormous muscle bundles. As the intervertebral rotation occurs around the articulation between the condyle and the cotyloid cavity, the extension of the neural spine assures a maximum length of moment arm for the muscles attaching to this member. Though extremely fragile in a lateral direction (a thin bone will take up only a small portion of the space available to the muscles), the neural spine is structurally quite strong, and as it possesses a deep cross section along the longitudinal axis of the snake, it can easily carry the forces imposed on it in this direction. The aliform processes and the heavy fascia sheathing the dorsal musculature both serve to prevent lateral slippage of the muscles. This is very important during the periods when the vertebral column is bent into a sharp curve, as the muscles, which are then in considerable tension, would possess a natural tendency to form the shorter chord rather than the arc of the circle. The whole arrangement of the two deep troughs tends to inhibit this and to retain the muscles at the site of their maximum effectiveness. The sheet of fascia thus takes over the function of the skin, which to facilitate expansion is mainly tied along the mid-dorsal.

The blunt or faintly ridged intermediate hypapophyses serve as stress concentrating points, transmitting the action of the dorsal and lateral muscles to the shell and assuring that the main rupture takes place mid-dorsally. While attempts to make detailed deductions from the appearance and the fracture lines of the crushed shell have failed in the past (Howes, 1901, p. 320), examination of several such shells has given confirmation to suppositions regarding the function of the intermediate vertebrae. When the shell first cracks, the squeezing of the encompassing musculature causes a number of longitudinal fracture lines. The blunted hypapophyses of the intermediate hypapophysials cause the major failure of the egg, and an inward folding of the shell takes place along the hypapophysial ridge. This folding continues as the chushing effect slowly reduces the egg's diameter, so that the final remains constitute the "boat-shaped" residue mentioned by many authors. This inward folding initiated by the hypapophyses is important in that it assists in packing the fragments of egg shell into a relatively straight sided and compact bundle, which is easily managed during ejection and contains only a minimum amount of egg fluid.

It is obvious that the more sharply ridged hypapophyses of juvenile specimens allow the imposition on the egg shell of an equivalent stress concentration with a much lower energy input, thus suiting the snake's limitations much better than would the rounded knobs of the adult animal. The reduction of the stress concentration is of no particular importance to the adult, whose muscles are amply large enough to provide the additional force required to crush the shell. Here the problem lies rather in the construction of the hypapophyses, since these have to withstand and repeatedly transmit the high forces imposed by the tremendously developed musculature.

The strong compression exerted upon the egg squeezes out its contents, which slowly flow into the stomach through the constricted posterior esophagus. The bands of the anterior portion of the *M. retractor quadrati,* forming the *Sphincter colli,* effectively close off the throat, thus assuring that no fluid can flow anteriorly. The probability of such escape has also been made extremely unlikely by the inward folding of the shell, which leaves the partly emptied egg sufficiently entire to allow it to act as a seal to prevent loss of its contents towards the mouth of the snake. As part of the egg's contents may be rather viscous, considerable pressure is necessary to force the contents through the very narrow opening into the stomach.

*Ejecting.*—Manifold references in the literature state that the posterior hypapophyses do not serve to break the shell, but that they rather function to prevent the crushed shell from slipping down the esophagus, retaining the shell in a position from which it may be regurgitated. Examination of the relative sizes of the esophagus, and of the posterior hypapophyses will immediately convince anyone of the infeasibility of this claim, particularly since the posterior spines are located in a region where the esophagus is still fully expansible.

The ability of most snakes to regurgitate food from the esophagus and even from the stomach has been referred to previously, in discussing the habits of this form. The ejection of recently ingested or even partially digested food items seems to be designed to allow the snakes unrestricted motility for escape or defense at times of danger, an attribute shared with a number of other animals that are also known to gorge themselves to the point where they are almost immobile. In all snakes observed this ejection is accomplished in an identical manner, which to judge from the photographs is also shared by *Dasypeltis.*

In ejecting, the snake gapes widely and relaxes the anterior lateral musculature. Simultaneously the spine forms a tight S-shaped curve just posterior to the food object. As this S-curve moves forward, the attendant constriction of the body cavity moves the contents of the esophagus ahead of it. In some snakes the head and neck simultaneously engage in a rapid whiplike lateral motion, so that the food literally seems to shoot out of the mouth. A previously unpublished photograph of Dunton's, taken at the start of ejection (Plate IV, Fig. 7), shows the specimen with gaping mouth, the S-curve formed, and the anterior body "whipping," all these definitely documenting the fact that ejection here proceeds in the same general manner as in other snakes. It may just be stated in passing that the requirement that the vertebrae possess sufficient lateral rotational freedom to permit formation of the S-curve imposes another condition on the already highly modified intermediate vertebrae and accounts for the large articulating facets on the zygapophyses.

As stated above most snakes only utilize this method of ejection to empty the alimentary canal in times of danger. This simplifies the process in that no selectivity has to be involved and the entire contents of the stomach and esophagus may be disgorged. In *Dasypeltis,* however, the matter is somewhat more complicated since it is desired to eject the shell only. Selectivity thus becomes extremely important, particularly after the specimen has eaten a number of eggs and the stomach is distended with fluid. It is here that another modification of the severe restriction of the posterior esophagus, which has two basic functions, becomes apparent.

The structure is formed of an elongate, decidedly non-elastic tube, which is surrounded by a collar of smooth muscle first demonstrated by Kathariner (1898, p. 518, f. 9), which acts as a valve in preventing the loss of fluid from the stomach during ejection. The repeated convulsive squeezing of the neck region against the ground with simultaneous arching of the section posterior to this, mentioned by Durham, thus indicate a squeezing of the egg as well as a forcing of the egg fluid toward the posterior end of the stomach. After the snake has completely emptied the shell and immediately subsequent to the completion of one of the convulsive contractions, the ring muscles close the valve simultaneously with the formation of the S-curve behind the shell's location. Since the end of the S-curve naturally extends beyond the heart, these contractions also momentarily force back the stomach's contents, thus reducing the hydrostatic pressure on the esophageal valve and increasing the chances that this valve might successfully retain the fluid until the S-curve had passed into the intermediate hypapophysial region.

The esophageal valve also possesses a second most important function, in that it assures that neither the egg nor the crushed shell can ever escape from the retaining muscles and slip back far enough to reach the heart. This is of great importance as the body cavity is not large enough at this point to accommodate both the heart and an egg, even if the shell of the latter has first been crushed. There are several reports indicating that large North American snakes of such genera as *Elaphe* and *Pituophis* have died supposedly from the effects of ingesting china nest eggs. I am not completely convinced of the authenticity of such reports, but should be inclined to give them the benefit of the doubt, as it would appear quite possible that the snake, failing in its initial effort to crack the egg, would attempt to pass it into the stomach. If the egg were of sufficient size this might well rupture the heart or tear it loose from its connecting blood vessels, with fatal results. In *Dasypeltis,* however, such action would be entirely impossible because of the esophageal constriction, so that no reason exists for believing similar tales concerning this snake, no matter how much embellished.

The method of regurgitation utilized by *Dasypeltis* again points out the advantage obtained from the inward folding of the shell. In spite of its very thin and brittle nature, egg shell is sufficiently hard and strong to cause serious injury to the esophageal lining during the ejection of large and jagged pieces of shell. The inward folding assures that all pieces, joined by the adhering internal shell membranes, are ejected as a blunt bundle with almost no sharp edges. Only small chips accidently broken away from the membrane and sufficiently tiny to pass the posterior esophagus can ever find their way into the stomach.

Since the ejection of the shell completely clears the esophagus, the snake is immediately ready to attack the next egg in the nest.

## SUMMARY

In this paper the ingestion, cracking, crushing and ejecting sequence has been completely reexamined for the snakes of the genus *Dasypeltis,* on the basis of more than 100 specimens, with the primary emphasis being placed upon a functional analysis of the structures involved. Various previously neglected and unknown modifications are described and the function of many other structures is submitted to a new interpretation.

Modifications are covered which allow the snake to swallow eggs with a diameter more than twice the specimen's height of gape, in which way this form differs from all other snakes (with the possible exception of *Elachistodon westermanni*).

The dentitional reduction and several modifications of the jaws and mucosa which tend to compensate for this are described, and their functions are discussed in detail. It is pointed out that loss of teeth is not necessarily of adaptive value for the ingestion of eggs.

The morphology and function of the anterior vertebrae is discussed in detail. It was found that

the initial fracture of the egg is effected by the piercing action of the posterior hypapophyses with the intermediate hypapophysials serving to crush the egg and squeeze its contents into the stomach. The function of the anterior hypapophyses of other snakes is also reinterpreted.

The axial musculature was found to be greatly developed and to function by crushing and emptying the egg, while the posterior esophagus is modified into an esophageal valve serving to retain the ingested egg fluid during the ejection of the empty shell.

These findings indicate that this snake is far more highly specialized than had previously appeared. The form exhibits an extreme degree of adaption to the ingestion of a single food item, namely avian eggs. As these are available only once or twice a year (during the two breeding seasons in regions of Africa) it becomes necessary for this rather retiring form to be able to store fat for the remainder of the year. The ability of specimens to regurgitate the bulky egg shell permits the rejection of bulk of a strictly non-nutritive nature and prevents waste of digestive juices and intestinal space normally required for its disposal. The result may well be an increase of fifteen to thirty per cent in the food capacity of the form. As only a limited number of nests can be visited during the period in which eggs are available, this reflects directly on the quantity of food the species can store as fat.

A high degree of variation was noted among the morphological characters examined, indicating the desirability of basing similar morphological analyses upon as large a series as possible.

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## EXPLANATION OF THE PLATES

### PLATE I

FIG. 1. *Dasypeltis* examining egg prior to attempt at ingestion.

FIG. 2. Initiation of ingestion process. Note the separation of mandible and labials, the sharp bend of the ventral band and the contraction of the neck musculature sliding this forward.

### PLATE II

FIG. 3. Snake with egg partially engulfed. The S-curve of the neck forces the egg against the stabilizing coil of the body. There is almost no evidence of the deformation and spreading of the upper jaw normally apparent in snakes during ingestion.

FIG. 4. The mandibular tips are joining and the mouth closes as the egg is forced into the esophagus.

### PLATE III

FIG. 5. Egg in position with the posterior, piercing hypapophyses being brought into action. The sharp bend of the spine just posterior to the egg is clearly apparent.

FIG. 6. The pierced egg has been crushed and partially emptied.

### PLATE IV

FIG. 7. Undulation and gaping just prior to ejection of empty shell.

FIG. 8. Appearance of ejected shell, showing the joining of the fragments by the shell membrane.

Note: All photographs made in the New York Zoological Park by Sam Dunton, Staff Photographer.